



1	A global meta-analysis of rhizosphere impacts on soil and microbial
2	stoichiometry in agroecosystems
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Abstract. The stoichiometry of the rhizosphere, particularly concerning carbon (C), nitrogen (N), and phosphorus (P), reflects the balance between nutrient mineralization and retention during organic matter decomposition. However, the magnitude and underlying mechanisms of rhizospheric influences on soil and microbial stoichiometry remain insufficiently quantified at the global scale across diverse agroecosystems. This study synthesizes data from 113 peer-reviewed sources, encompassing 882 individual observations. The results reveal that the rhizosphere significantly increases soil C:N, C:P, and N:P ratios, while concurrently decreasing microbial C:N, C:P, and N:P ratios relative to bulk soil conditions. Notably, the rhizospheric effects on soil C:N ratios is amplified in humid regions and diminished in arid environments. In contrast the influence on microbial C:N exhibits a positive correlation with increasing soil organic C and ammonium N concentrations. Moreover, sensitive crops such as maize and vegetables enhance the rhizospheric soil C:N ratio by 5.68% and 8.91% respectively, while reducing the microbial C:N ratio by 11.00% and 19.44%. Soil organic C and ammonium N emerge as key determinants of rhizospheric soil and microbial C:N ratios, contributing 37.9% and 30.3% to their varations, respectively. The study establishes a coupled relationship between rhizospheric soil and microbial stoichiometry. These findings offer critical insights into rhizospheric nutrient cycling, which are essentials for improving soil health and optimizing nutrient use efficiency through targeted management practices.





1 Introduction

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2022). As key determinants of agricultural productivity, soil nutrients play a pivotal role in regulating microbial community compositions and enhancing crop yields (Cai et al., 2019). The rhizosphere soil, a distinct micro domain influenced by root a activity, differs physically, chemically, and biologically from bulk soil (Berendsen et al., 2012). The nutrient status of the rhizosphere, including carbon (C), nitrogen (N), and phosphorus (P), is critical in regulating root exudates, soil material cycling, energy flow, and signal transmission, thereby profoundly impacting plant growth and development (Gan et al., 2021). Compared to bulk soil, the dynamic environment of the rhizosphere significantly affects nutrient availability and microbial interactions, which are critical for plant health and productivity. In agroecosystems, rhizospheric nutrient dynamics are particularly sensitive to rapid crop growth and anthropogenic disturbances, rendering than in natural terrestrial ecosystems. Therefore, a systematic understanding of rhizospheric nutrient behavior is essential for maintaining agroecosystem health and promoting sustainable agricultural practices globally. This knowledge is vital for developing strategies that enhance soil fertility, optimize nutrient use efficiency, and support sustainable crop production. Ecological stoichiometry, a discipline focused on the balance and interactions of key elements in ecosystems, has provided valuable insights into individual growth population dynamics, limiting factors, community succession, and vegetation stability (Güsewell, 2004). understanding individual growth (Güsewell, 2004). Soil C:N:P ratios vary significantly due to differences in vegetation type and soil organic matter content (Luo et al., 2020). Microbial communities respond to stoichiometric changes in four primary ways: First, adjusting biomass composition to match available resources, though these changes are generally modest and driven more by shifts in microbial community structure than by cellular storage. Second, mobilizing resources via enzyme production, which is often limited by C and N availability (Ashraf et al., 2021). Third, regulating element use efficiency allow for the release of excess nutrients. Fourthly, utilizing diastrophic bacteria and saprotrophic fungi to acquiring exogenous N and P (Mooshammer et al., 2014). Globally, current knowledge on soil and microbial biomass stoichiometry is primarily focused on bulk soil (Luo et al., 2020). However, rhizospheric nutrients and microbial communities are more susceptible to environmental fluctuations than those in bulk soil. Thus, a comprehensive understanding of rhizospheric characteristics and their interactive

Agroecosystems constitute approximately 40% of all terrestrial ecosystems on Earth, making them a

critical infrastructure that significantly influence the planet's health and sustainability (Dubey et al.,

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64 insight is critical for developing strategies that enhance soil fertility, optimize nutrient use efficiency, and support sustainable agricultural practices worldwide. Environmental factors, nutrient inputs, and agricultural practices significantly influence the stoichiometry of rhizospheric soil and microbial biomass (Luo et al., 2020; Yue et al., 2017). Studies have shown that soil C:nutrient (N and P) ratios decline in arid regions,, while soil P ratio tend to be lower in wetter environments (Feng et al., 2019). This reduction in arid conditions is attributed to increased carbon use efficiency and a greater proportion of C being converted into microbial biomass under carbon limited conditions. Agroecosystem management strategies affect the rhizospheric 72 stoichiometry by influencing microbial biomass, enzyme activities, and nutrient availability (Lasota et al., 2021). The stoichiometric ratios of C:N and C:P in soil, as well as their microbial counterparts, vary 74 significantly across habitats (Khan et al., 2016; Qi et al., 2022). These variations are primarily influenced microbial nutrient demand and availability, which are affected by factors such as soil pH, 76 salinity, clay content, and organic matter uptake (Khan et al., 2016; Lian et al., 2021; Lu et al., 2018). High C availability, especially when coupled with limited P, leads to increased microbial biomass and 78 elevated microbial C:N ratios (Du et al., 2022; Hou et al., 2018). Strongly acidic, nutrient-poor soils with high C: N and C:P ratios are also associated with elevated microbial C:N ratios (Khan et al., 2016). However, comprehensive data on how environmental variables influence rhizospheric soil and 81 microbial stoichiometry in agroecosystems remains limited. Addressing this knowledge gap is essential 82 for developing strategies to optimize nutrient efficiency and enhance soil health in diverse agricultural 83 contexts. 84 Although previous studies have extensively examined the C:N:P stoichiometry in soils, plants, and microbes across natural and managed ecosystems, agricultural rhizospheric soils are often 86 underrepresented. To fill this gap, we compiled a comprehensive dataset comprising 882 unique cases from 113 peer-reviewed sources across global agroecosystems. The objectives of this study were to: (1) quantify the characteristics and coupling relationships of rhizospheric soil and microbial biomass stoichiometry across global agroecosystems; and (2) identify the environmental factors influencing rhizospheric soil and microbial biomass stoichiometry. 2 Materials and Methods

stoichiometric interactions is crucial for improving agroecosystem productivity and management. This

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2.1 Database collection and assembly

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To evaluate the ecological stoichiometry of rhizospheres across diverse plant species, a high-resolution approach was employed to correlate plant community composition with below-ground microbial and nutrient properties. This methodology facilitated the development of stoichiometric models that investigate the effects of climatic and agricultural variables on the rhizospheric stoichiometry of carbon (C), nitrogen (N), and phosphorus (P) in both bulk and rhizospheric soils (Bell et al., 2014; Cui et al., 2018). The dataset for this study was compiled from three major databases: Google Scholar, Web of Science, and China Knowledge Resources Comprehensive Database. The search utilized a combination of keywords, including "stoichiometry", "rhizosphere", "soil properties", "soil organic carbon", "soil microbial biomass", and "cropland, farmland, or agriculture". Specific inclusion criteria were applied to ensure the retrieval of relevant literature and compilation of a standardized dataset. To elucidate the effects of the rhizosphere on soil and microbial biomass stoichiometry of C, N, and P the following criteria and data acquisition processes were rigorously followed (1) The study must have been conducted within an agricultural ecosystem; (2) The literature must include paired data (rhizosphere, non-rhizosphere, or bulk soil), where the treatment and control groups represent rhizosphere and non-rhizosphere (bulk soil), respectively; (3) Each experiment must have included at least three plots as replicates; (4) The paired data must report at least two elements among C, N, and P for both soil and microorganisms. Experimental data reported in tables and text was directly recorded into the dataset. Data presented in figures were digitized using GetData Graph Digitizer 2.24 to ensure accuracy. A comprehensive dataset was compiled, comprising 822 individual cases derived from 113 relevant literature sources published up to September 2022. A detailed flow diagram outlining the selection process for the target literature is provided in supplementary figure S2. Soil biogeochemical variables were recorded to analyze the spatial distribution characteristics of rhizospheric effects on C, N, and P stoichiometry across various climate conditions, including mean annual temperature [MAT], mean annual precipitation [MAP], aridity index [AI], and crop types. Additionally, soil attributes were incorporated into the database to explore variations in rhizospheric effects on C, N, and P stoichiometry. Key indicators included soil pH, nitrate-N (NO₃-N), ammonium-N (NH₄+N), and available phosphorous (AP). 2.2 Data preparation For the 882 individual cases, 75% of the latitude and longitude data were directly recorded from the

targeted literature, while the missing 25% were obtained using Google Maps. Climatic variables,

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including mean annual temperature (MAT), mean annual precipitation (MAP), and aridity index (AI), were extracted from the targeted literature for 76% of the cases, and with the remaining 24% sourced from WorldClim (https://worldclim.org/), respectively. The experimental sites covered a wide range of latitudes, from -7.14 ° to 60.46 ° and longitudes from -113.99 ° to 126.58 °. The climatic variables, specifically MAT, MAP, and AI varied from -3.48°C to 26.97°C, 32 mm to 1926 mm, and 0.02 to 1.54, respectively. Soil texture components including sand, silt, and clay varied between 7.51 to 60.50%, 12.10 to 92.00%, and 7.72 to 69.50%, respectively. Detailed site data for the selected climate conditions and soil textures are provided in supplementary table S1. For studies reporting soil organic matter, soil organic C (SOC) concentrations were calculated using the equation: SOC = soil organic matter/1.724. To comprehensively analyze the spatial heterogeneity of rhizospheric effects on C, N, and P stoichiometry, two classification techniques were applied based on the geographic location of the experimental sites (Xu et al., 2021). First, the experimental sites were categorized into four climatic regions according to absolute latitude: tropical zone with 0-23.5°, subtropical zone with 23.5-35.0°, temperate zone with 35.0-50.0°, and (sub)arctic zone with >50.0°. Second, the experimental sites were grouped into four categories based on AI levels: ≤ 0.20, 0.20-0.65, 0.65-1.0, >1.0, corresponding arid, semi-arid, sub-humid, and humid, respectively. The crop types were classified into six main groups: wheat, maize, rice, soybean, vegetables (e.g., green vegetables, celery, tomatoes, radishes, cucumbers, and lettuce), and others (e.g., cotton, rape, potato, pasture, etc.). The SOC concentrations (g kg⁻¹) in bulk soil were categorized into three levels (0-8.0, 8.0-16.0, and >16.0). Bulk soil pH was divided into four categories i.e. ≤ 5.5 , $5.5 < pH \leq 6.5$, $6.5 < pH \leq 7.5$, and 7.5 < pH. The soil ammonium nitrogen concentrations (mg kg⁻¹) were also divided into four categories NH_4^+ - $N \le 1.0$, $1.0 < NH_4^+$ - $N \le 5$, 5 < NH_4^+ -N ≤ 10 , and $10 < NH_4^+$ -N. 2.3 Statistical analysis The "metafor" package in R, incorporating mixed effects models, was used to quantify the rhizospheric effects on soil and microbial stoichiometry (Cai et al., 2021; Xu et al., 2021). Funnel plots (S3) were employed to assess publication bias, revealing no significant bias (P > 0.05). To examine the influence of environmental variables on disparities between rhizospheric effects on soil and microbial stoichiometry, certain factors were initially excluded based on Pearson's correlation and stepwise regression analyses to avoid multicollinearity (S4 and 5). Linear regression was employed to assess the

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relationship between rhizospheric effects on the soil C:N, C:P, and N:P ratios (S6). However the sample sizes for rhizospheric effects on microbial C:P and N:P were limited (57 and 29) samples, respectively. Consequently, we focused on analyzing the drivers and attributes of rhizospheric effects on soil and microbial C:N ratio. Boosted regression tree (BRT) analyses was performed to quantify the relative influence (%) of environmental variables on rhizospheric effects on soil and microbial C:N ratios, accounting for nonlinear relationships (Cai et al., 2019; Elith et al., 2008). Prior to BRT analyses, highly correlated factors were excluded using Pearson's correlation to minimize multicollinearity. The BRT models were implemented with the following optimized parameters: learning rate (0.01), bag fraction (0.50), cross-validation (10), and a tree complexity (5). The BRT predicted rhizospheric effects on soil and microbial C:N ratios were compared with observed values. The coefficient of determination (R 3 was used to evaluate the predictive power of the selected factors. All BRT models were executed using the GBM package and the methodology outlined by Elith et al. (2008) in R version 4.1.5. 3 Results 3.1 Overall rhizospheric effects on soil and microbial stoichiometry The median values of soil C:N (10.50), C:P (15.42), and N:P (1.46) ratios in the rhizosphere were higher than those in bulk soil (10.10, 12.92, and 1.36 respectively) (Fig. 1). In contrast, the median values of microbial C:N, C:P, and N:P ratios in the rhizosphere were lower, at 7.99, 13.52, and 2.42, respectively. As a result, rhizospheric effects led to significant increases in soil C:N, C:P, and N:P ratios by 5.13%, 6.48%, and 4.01%, respectively, while significantly decreasing microbial C:N, C:P, and N:P ratios by 1.94%, 11.53%, and 10.01%, respectively (Fig. 2). 3.2 Rhizospheric effects on soil and microbial C:N ratios under various climatic variables Across different climate zones, rhizospheric effects on soil C:N ratios increased significantly by 9.49% in tropical zones, 5.76% in subtropical zones, and 3.39% in temperate zones, (Fig. 3a). Conversely, microbial C:N ratios declined cmarkedly by 20.19% in the tropical zone with no significant changes observed in the other climate zones (Fig. 3b). Under varying aridity levels, rhizospheric effects on soil C:N ratios increased by 3.27% in semi-arid and 7.36% n humid environments, respectively. In contrast, microbial C:N ratios significantly decreased by 21.47% under arid conditions, with no significant changes observed in other aridity levels. 3.3 Rhizospheric effects on soil and microbial C:N ratios under various soil properties and crop types





183 Regarding soil properties, rhizospheric effects on soil C:N ratios increased significantly by 6.5% and 184 11.86% at soil pH of ≤ 5.5 and 5.5-6.5, respectively (Fig. 4a). These effects decrease exponentially 185 with increasing SOC, ranging from 3.39% to 8.39%. Conversely, rhizospheric effects on microbial C:N 186 ratios increased linearly with rising SOC and soil NH₄⁺-N concentrations (Fig. 4b). Microbial C:N ratios decreased significantly by 9.41% and 7.29% when NH₄⁺-N was ≤ 1 and SOC was ≤ 16 respectively 187 188 (Fig. 5). Different crop types (e.g., rice, maize, vegetables, and other crops) enhanced rhizospheric 189 effects on soil C:N ratios by 3.79%, 5.68%, 8.91%, and 8.07%, respectively (Fig. 5a). In contrast, the 190 rhizosphere significantly reduced microbial C:N ratio by 19.44% and 11.00% for vegetables and maize, 191 respectively (Fig. 5b). 192 3.4 Mechanisms of rhizospheric effects on soil and microbial stoichiometry 193 According to the boosted regression tree model, the selected environmental variables explained 83% 194 and 75% of the variation in rhizospheric effects on soil and microbial C:N ratios, respectively, (Fig. 6). 195 Among these SOC (37.9%) and soil pH (20.7%) were the most influential for soil C:N ratios (Fig. 6a), 196 while soil NH₄₊-N (30.3%) and SOC (19.5%) were the most influential factors microbial C:N ratio (Fig. 197 6b). Additionally crop type and aridity index emerged as secondary factors in influencing rhizospheric 198 effects on both soil and microbial C:N ratios. 199 A network of inter-correlations was observed among rhizospheric effects on soil and microbial 200 stoichiometry (Figs. 7 and S5). Rhizospheric effects on soil C:N ratios were positively correlated with 201 those on soil C:P ratios, and negatively correlated with those on soil N:P ratios. Similarly, rhizospheric 202 effects on soil C:P and N:P ratios were positively correlated microbial N:P ratios were positively 203 correlated with microbial C:P ratios and negatively correlated with microbial C:N ratios. The SOC 204 showed a significant positive correlation with rhizospheric effects on soil C:N and C:P ratios and a 205 negative correlation with soil NH₄⁺-N. In turn, soil NH₄⁺-N was positively correlated with rhizospheric 206 effects on microbial N:P ratios and negatively correlated with microbial C:N ratios. 207 4 Discussions 208 Positive rhizospheric effects on soil C:N, C:P, and N:P ratios were consistently observed across all 209 samples (Fig. 1 and 2). This effects may be attributed to C inputs from root exudates and decaying 210 roots through rhizodeposition, which typically exhibit relatively high C:N ratios (Fontaine et al., 2011). 211 Rhizodeposition promotes soil macro-aggregate, formation, a critical process for soil organic carbon 212 sequestration and decomposition (Li et al., 2020). It also contributes additional N for microbial growth,

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supporting microbial biomass formation, while exerting a limited impact on soil TN. Root exudates (e.g., amino acids, phytosiderophores, or inorganic ions) can induce P mineralization in the rhizospherse, thereby enhancing P uptake by crops (Dotaniya and Meena, 2014). These findings suggest that rhizospheric effects facilitate SOC turnover and create a favorable microenvironment rich in essential nutrients for crop development (Kuzyakov and Razavi, 2019). However, limited data on root exudates in our database constrained further analysis of their specific impact on soil and microbial stoichiometry. Thus, further research is necessary to elucidate the roles of root exudates in modulating rhizospheric responses related to soil and microbial stoichiometry. Interestingly, negative rhizospheric effects on microbial stoichiometry were observed (Fig. 1 and 2), indicating lower microbial C:N:P ratios i in the rhizosphere compared to bulk soils. These reductions likely stem from altered nutrient availability and enriched living environment in the rhizosphere. In agroecosystems, the application of readily available inorganic nutrients can disrupt natural nutrient cycles leading to significant shifts in microbial C:N:P ratios, especially in nutrient-poor soils (Griffiths et al., 2012). These changes are potentially due to shifts in microbial community composition (Heuck et al., 2015). Previous research suggests that under nutrient-limited conditions, microbial communities may transition from r-strategists to k-strategists, capable of decomposing more stable organic matter to access organic N or P thereby increasing mineralization of soil organic matter (Chen et al., 2014; Zhu et al., 2018). Furthermore, microbial cells formation requires P-rich phospholipids, contributing to a substantial phosphorus demand. Overall, these findings highlight the variability in rhizospheric influences on soil and microbial stoichiometry in agroecosystems, with the magnitude of these effects being shaped by climate, crop type, and soil characteristics. The rhizospheric effects on soil C:N ratios were 9.49% in tropical, 5.76% in subtropical, and 3.39% in temperate, respectively. However, microbial C:N ratios were significantly affected only in the tropical zones (20.19%) and showed no marked changes in other climatic regions (Fig. 3). These differences may be attributed to variations in crop residue decomposition rates, anthropogenic influences, temperature, and moisture availability (Wang et al., 2014). Typically, temperate soils are N-limited, while tropical soils are primarily P-limited due intense weathering, older soil profiles, and the abundance of Fe and Al oxides (Du et al., 2022; Soong et al., 2018). Three mechanisms may explain the increased soil C:N ratios under varying climatic conditions. First, plant litter may stimulate microbial respiration, thereby increasing microbial C and N contents (Soong et al., 2018). Second, the

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application of organic and inorganic nutrients provides C and energy for microbial growth, population, and activities. Third, microbial community composition may shift under nutrient constraints, such as alterations in fungal:bacterial ratios or microbial diversity in general (Zhu et al., 2018). In semi-arid and humid environments, rhizospheric effects on soil C:N ratios increased by 3.27% and 7.36%, respectively(Fig. 3b). This could be related to the high organic material content and compaction (high bulk density) in the studied soils (Wang et al., 2014). With increasing aridity and warming, soil C:P and N:P ratios tend to decrease, while soil C:N ratios rise, reflecting projected precipitation declines and warming trends in semi-arid regions (Jiao et al., 2016). Soil C accumulation may result from two mechanisms (Yu et al., 2018). First, climate change has boosted net primary productivity terrestrial ecosystems (Yu et al., 2018). Second, nitrogen deposition increases soil acidity, decelerates litter decomposition, and reduces soil respiration, all of which promote SOC buildup (Yu et al., 2018). Meanwhile, under arid conditions, the microbial C:N ratio in the rhizospheric decreased by 21.47% relative to bulk soils (Fig. 3b), potentially due to lower total organic matter and nutrient availability. Collectively, these findings highlight the pivotal role of climate in regulating rhizospheric impacts on soil and microbial stoichiometry, with microbial C:N ratios being more sensitive than their soil counterparts. The responses of nutrient stoichiometry to rhizospheric influences varied significantly with crop type (Fig. 4). Vegetables and maize increased rhizospheric effects on soil C:N ratios by 8.91% and 5.68%, respectively (Fig. 4a). Generally, vegetables and maize typically exhibit high nitrogen demand during growth, which may reduce the contribution of external nitrogen sources to total soil nitrogen (Tei et al., 2020). Conversely, leguminous crops fix atmospheric nitrogen via root nodules, resulting in lower nitrogen during early growth stages (Fig. 4a). It has been suggested that N₂O emissions could be reduced by approximately 60% with current emissions attributed to maize (33%) and vegetable production (27%) (Cui et al., 2022). Compared to bulk soils, C₄ crops (maize and partial vegetables) lead to relatively lower soil N concentrations in the rhizosphere (Bell et al., 2014). Interestingly, the microbial C:N ratio in the rhizosphere significantly decreased for vegetables and maize (Figs. 2b, 3b). This may be due to microbial decomposition of SOC into labile substrates such as mineralized glucose (Siles et al., 2022). Crop residue inputs from these systems enhance SOC levels through microbial stoichiometric plasticity mechanisms (Liu et al., 2014); enriching soil C pools by modifying microbial stoichiometry in C-limited conditions. Elevated C:N ratios suggest that soil organic matter tends to

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accumulate more rapidly than it decomposes (Chen et al., 2018). Reduced microbial C:N and C:P ratios promote nutrients release by microbes, increasing bioavailable N and P. In contrast, higher microbial C:N and C:P ratios may lead to microbial competition for nutrients, enhancing N and P immobilization in the soil (Chen et al., 2014). The SOC and pH were the most influential factors affecting rhizospheric soil C:N ratios (Fig. 6a), likely due to their direct effects on microbial function and organic matter retention by the soil matrix (McMillan et al., 2016). Increased acidity can alter SOC quality and composition (Kemmitt et al., 2006). Improved SOC retention at low pH levels may result from decreased microbial biomass and activity, higher organic matter stabilization, and complication with polyphenols and aluminum (Kemmitt et al., 2006; McMillan et al., 2016). The decomposition of organic residues also increases soil pH through the breakdown of alkaline anions and nitrate uptake by microbes, releasing hydroxyl ions (Bertrand et al., 2007). These findings suggest that acidic rhizospheric soils support higher SOC accumulation and elevated C:N ratio. Furthermore, NH₄⁺-N and SOC were key drivers of microbial C:N ratio in the rhizosphere (Fig. 6b). Microbial activity regulated by SOC availability can affect carbon accumulation (Angst et al., 2018; Sistla and Schimel, 2012). According to the stoichiometric decomposition theory, microbial decomposition and nutrient release are governed by the elemental balance between microbial biomass and organic matter. However, under nutrient-limited conditions, microbial processes are constrained, which in turn limits SOC breakdown (Sistla and Schimel, 2012; Zhu et al., 2018). Root nitrogen uptake can further alter rhizospheric pH and stimulate root exudation, influencing microbial community composition and function. Stronger rhizospheric effects on microbes are observed in soils with low N availability (Phillips and Fahey, 2008). Thus, soil management strategies, such as the application of ammonium fertilizers, may be employed to enhance microbial C:N ratios. Moreover, the inverse relationship between N mineralization and microbial C:N ratio suggests that microbial immobilization of mineral N contributes to its depletion (Dai et al., 2020). The negative correlation between C and microbial C:P ratio may be due to a larger cumulative priming effect and microbial P limitation. Microbes increase phosphorus uptake to maintain internal stoichiometric balance (Wei et al., 2020; Wei et al., 2019). The soil C:N ratio was positively correlated with C:P ratios, and negatively correlated with N:P ratios (Fig. 8). The observed link between microbial and soil C:N:P ratio implies non-homeostasis elemental stoichiometry in microbial biomass (Li et al., 2012), indicating that these ratios influence C stabilization in surface soils (Angst et al., 2018). The addition of fresh

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organic amendments like manure can strongly impact SOC and N mineralization, as well as induce variable priming effect, either positive or negative (Zhu et al., 2018). Aridity also plays a critical role in modulating soil C:N:P ratio, potentially disrupting biogeochemical cycling. With increased aridity and altered soil textures C, N, and P cycles become more sensitive to climate change due to shifts in particle size and the decoupling of soil C, N and P ratios (Jiao et al., 2016; Wang et al., 2020). High soil C content elevates the C:N ratio, while it markedly reducing the N, P, and N:P ratio. The significant negative correlation between C:N and C:P ratios, and OC content, indicates that that mineral-rich soils with lower organic matter are often enriched in P. These results contribute to a more comprehensive understanding of soil property-mediated regulation of rhizospheric C, N, and P cycling in agroecosystems. 5 Conclusions

Our global synthesis confirmed that the rhizosphere significantly increases soil stoichiometry while decreasing microbial stoichiometry compared to bulk soil in agricultural ecosystems worldwide. Notably, rhizospheric effects on the soil C:N ratio were more pronounced in humid regions, whereas effects on microbial C:N ratios were more strongly reduced in arid regions then in other climatic zones. Greater rhizospheric effects on soil C:N ratios and lower effects on microbial C:N ratios were observed in vegetables and maize cropping systems. The rhizospheric impact on soil C:N ratios showed an exponentially decreasing trend with increasing SOC, whereas the effects on microbial C:N ratios exhibited a linear increase with SOC and soil NH₄⁺-N. Our findings further revealed that SOC and NH4+-N were the primary and most important drivers of rhizospheric soil and microbial C:N ratios, respectively. A significant coupling relationship was also found between the stoichiometric responses of soil and microbial communities to rhizospheric effects. Collectively, these results highlight inconsistencies in rhizospheric effects on soil and microbial stoichiometry regulation in agroecosystems, providing insights for improving resource efficiency and sustainable agricultural development through appropriate regulatory measures.

Author contribution

329 TF and AD: Conceptualization, Methodology, Data curation, Software, Writing-original draft. SN, TJ, 330 and W carried the data collection and analysis. AD: Funding acquisition, Supervision; All authors: Data 331 curation, Investigation.

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Cai, A., Liang, G., Yang, W., Zhu, J., Han, T., Zhang, W., Xu, M., 2021. Patterns and driving factors of

litter decomposition across Chinese terrestrial ecosystems. J. Clean. Prod. 278, 123964.

Res. 189, 168-175. https://doi.org/10.1016/j.still.2018.12.022.





363 https://doi.org/10.1016/j.jclepro.2020.123964. 364 Chen, R.R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X.G., Blagodatskaya, E., 365 Kuzyakov, Y., 2014. Soil C and N availability determine the priming effect: microbial N mining and 366 stoichiometric decomposition theories. Global Change Biol. 20. 2356-2367. https://doi.org/10.1111/gcb.12475. 367 368 Chen, X., Chen, H.Y.H., 2021. Plant mixture balances terrestrial ecosystem C:N:P stoichiometry. Nat. 369 Commun. 12, 4562. https://doi.org/10.1038/s41467-021-24889-w. 370 Chen, X., Ding, Z., Tang, M., Zhu, B., 2018. Greater variations of rhizosphere effects within 371 mycorrhizal group than between mycorrhizal group in a temperate forest. Soil Biol. Biochem. 126, 372 237-246. https://doi.org/10.1016/j.soilbio.2018.08.026. 373 Cui, X., Shang, Z., Xia, L., Xu, R., Adalibieke, W., Zhan, X., Smith, P., Zhou, F., 2022. Deceleration of 374 Cropland-N₂O Emissions in China and Future Mitigation Potentials. Environ. Sci. Technol. 56, 375 4665-4675. https://doi.org/10.1021/acs.est.1c07276. Cui, Y., Fang, L., Guo, X., Wang, X., Zhang, Y., Li, P., Zhang, X., 2018. Ecoenzymatic stoichiometry 376 377 and microbial nutrient limitation in rhizosphere soil in the arid area of the northern Loess Plateau, 378 China. Soil Biol. Biochem. 116, 11-21. https://doi.org/10.1016/j.soilbio.2017.09.025. 379 Dai, Z.M., Yu, M.J., Chen, H.H., Zhao, H.C., Huang, Y.L., Su, W.Q., Xia, F., Chang, S.X., Brookes, 380 P.C., Dahlgren, R.A., Xu, J.M., 2020. Elevated temperature shifts soil N cycling from microbial 381 immobilization to enhanced mineralization, nitrification and denitrification across global terrestrial ecosystems. Global Change Biol. 26, 5267-5276. https://doi.org/10.1111/gcb.15211. 382 383 Dotaniya, M.L., Meena, V.D., 2014. Rhizosphere effect on nutrient availability in soil and its uptake by 384 plants: A review. P. Natl. A. Sci. India B. 85, 1-12. https://doi.org/10.1007/s40011-013-0297-0. 385 Du, J.X., Liu, K.L., Huang, J., Han, T.F., Zhang, L., Anthonio, C.K., Shah, A., Khan, M.N., Qaswar, M., 386 Abbas, M., Huang, Q.H., Xu, Y.M., Zhang, H.M., 2022. Organic carbon distribution and soil 387 aggregate stability in response to long-term phosphorus addition in different land-use types. Soil Till. 388 Res. 215, 105195. https://doi.org/10.1016/j.still.2021.105195. 389 Dubey, P.K., Singh, A., Merah, O., Abhilash, P., 2022. Managing agroecosystems for food and nutrition 390 security. Curr. Res. Environ. Sustain. 4, 100127. https://doi.org/10.1016/j.crsust.2022.100127. 391 Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 392 77, 802-813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.





- Feng, J., Wei, K., Chen, Z., Lü, X., Tian, J., Wang, C., Chen, L., 2019. Coupling and decoupling of soil
- 394 carbon and nutrient cycles across an aridity gradient in the drylands of northern China: evidence
- from ecoenzymatic stoichiometry. Global Biogeochem. Cy. 33, 559-569.
- 396 <u>https://doi.org/10.1029/2018GB006112</u>.
- 397 Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J.M.G., Maire, V., Mary, B., Revaillot, S.,
- 398 Maron, P.A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through
- 399 their priming effect. Soil Biol. Biochem. 43, 86-96. https://doi.org/10.1016/j.soilbio.2010.09.017.
- 400 Gan, D., Feng, J., Han, M., Zeng, H., Zhu, B., 2021. Rhizosphere effects of woody plants on soil
- 401 biogeochemical processes: A meta-analysis. Soil Biol. Biochem. 160, 108310
- 402 https://doi.org/10.1016/j.soilbio.2021.108310.
- 403 Griffiths, B.S., Spilles, A., Bonkowski, M., 2012. C:N:P stoichiometry and nutrient limitation of the
- 404 soil microbial biomass in a grazed grassland site under experimental P limitation or excess. Ecol.
- 405 Process. 1, 6. https://doi.org/10.1186/2192-1709-1-6.
- 406 Güsewell, S., 2004. N: P ratios in terrestrial plants: variation and functional significance. New Phytol.
- 407 164, 243-266. https://doi.org/10.1111/j.1469-8137.2004.01192.x.
- 408 Heuck, C., Weig, A., Spohn, M., 2015. Soil microbial biomass C:N:P stoichiometry and microbial use
- 409 of organic phosphorus. Soil Biol. Biochem. 85, 119-129.
- 410 <u>https://doi.org/10.1016/j.soilbio.2015.02.029.</u>
- 411 Hou, E., Chen, C., Luo, Y., Zhou, G., Kuang, Y., Zhang, Y., Heenan, M., Lu, X., Wen, D., 2018. Effects
- 412 of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. Global Change
- 413 Biol. 24, 3344-3356. https://doi.org/10.1111/gcb.14093.
- 414 Jiao, F., Shi, X.-R., Han, F.-P., Yuan, Z.-Y., 2016. Increasing aridity, temperature and soil pH induce
- soil C-N-P imbalance in grasslands. Sci. Rep. 6, 1-9. https://doi.org/10.1038/srep19601.
- 416 Kemmitt, S.J., Wright, D., Goulding, K.W., Jones, D.L., 2006. pH regulation of carbon and nitrogen
- 417 dynamics in two agricultural soils. Soil Biol. Biochem. 38, 898-911.
- 418 https://doi.org/10.1016/j.soilbio.2005.08.006.
- 419 Khan, K.S., Mack, R., Castillo, X., Kaiser, M., Joergensen, R.G., 2016. Microbial biomass, fungal and
- 420 bacterial residues, and their relationships to the soil organic matter C/N/P/S ratios. Geoderma 271,
- 421 115-123. https://doi.org/10.1016/j.geoderma.2016.02.019.
- 422 Kuzyakov, Y., Razavi, B.S., 2019. Rhizosphere size and shape: Temporal dynamics and spatial





- 423 stationarity. Soil Biol. Biochem. 135, 343-360. https://doi.org/10.1016/j.soilbio.2019.05.011.
- 424 Lasota, J., Małek, S., Jasik, M., Błońska, E., 2021. Effect of planting method on C:N:P stoichiometry in
- 425 soils, young silver fir (Abies alba Mill.) and stone pine (Pinus cembra L.) in the upper mountain
- 426 zone of Karpaty Mountains. Ecol. Indic. 129, 107905. https://doi.org/10.1016/j.ecolind.2021.107905.
- 427 Li, J., Yuan, X., Ge, L., Li, Q., Li, Z., Wang, L., Liu, Y., 2020. Rhizosphere effects promote soil
- 428 aggregate stability and associated organic carbon sequestration in rocky areas of desertification. Agr.
- 429 Ecosyst. Environ. 304. https://doi.org/10.1016/j.agee.2020.107126.
- 430 Li, Y., Wu, J.S., Liu, S.L., Shen, J.L., Syers, J.K., 2012. Is the C:N:P stoichiometry in soil and soil
- 431 microbial biomass related to the landscape and land use in southern subtropical China? Global
- 432 Biogeochem. Cy. 26, 4002. https://doi.org/10.1029/2012GB004399.
- 433 Lian, J.P., Liu, W.T., Meng, L.Z., Wu, J.N., Zeb, A., Cheng, L.P., Lian, Y.H., Sun, H.W., 2021. Effects
- 434 of microplastics derived from polymer-coated fertilizer on maize growth, rhizosphere, and soil
- properties. J. Clean. Prod. 318, 128571. https://doi.org/10.1016/j.jclepro.2021.128571.
- 436 Liu, S.L., Huang, D.Y., Chen, A.L., Wei, W.X., Brookes, P., C., 2014. Differential responses of crop
- 437 yields and soil organic carbon stock to fertilization and rice straw incorporation in three cropping
- 438 systems in the subtropics. Agr. Ecosyst. Environ. 184, 51-58.
- 439 <u>https://doi.org/10.1016/j.agee.2013.11.019</u>.
- 440 Lu, S., Lepo, J.E., Song, H.X., Guan, C.Y., Zhang, Z.H., 2018. Increased rice yield in long-term crop
- 441 rotation regimes through improved soil structure, rhizosphere microbial communities, and nutrient
- 442 bioavailability in paddy soil. Biol. Fert. Soils. 54, 909-923.
- 443 https://doi.org/10.1007/s00374-018-1315-4.
- 444 Luo, Xue, C., Jiang, Q., Xiao, Y., Ling, N., 2020. Soil carbon, nitrogen, and phosphorus cycling
- 445 microbial populations and their resistance to global change depend on soil C:N:P stoichiometry.
- 446 mSystems 5. https://doi.org/10.1128/mSystems.00162-20.
- 447 McMillan, A.M.S., Pal, P., Phillips, R.L., Palmada, T., Berben, P.H., Jha, N., Saggar, S., Luo, J., 2016.
- 448 Can pH amendments in grazed pastures help reduce N₂O emissions from denitrification? The
- 449 effects of liming and urine addition on the completion of denitrification in fluvial and volcanic soils.
- 450 Soil Biol. Biochem. 93, 90-104. https://doi.org/10.1016/j.soilbio.2015.10.013.
- 451 Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A., 2014. Stoichiometric
- 452 imbalances between terrestrial decomposer communities and their resources: mechanisms and





- 453 implications of microbial adaptations to their resources. Front. Microbiol. 5.
- 454 https://doi.org/10.3389/fmicb.2014.00022.
- 455 Phillips, R.P., Fahey, T.J., 2008. The influence of soil fertility on rhizosphere effects in Northern
- 456 Hardwood forest soils. Soil Sci. Soc. Am. J. 72, 453-461. https://doi.org/10.2136/sssaj2006.0389.
- 457 Qi, D., Feng, F., Lu, C., Fu, Y., 2022. C:N:P stoichiometry of different soil components after the
- 458 transition of temperate primary coniferous and broad-leaved mixed forests to secondary forests. Soil
- 459 Till. Res. 216, 105260. https://doi.org/10.1016/j.still.2021.105260.
- 460 Siles, J.A., Dáz-López, M., Vera, A., Eisenhauer, N., Guerra, C.A., Smith, L.C., Buscot, F., Reitz, T.,
- 461 Breitkreuz, C., van den Hoogen, J., Crowther, T.W., Orgiazzi, A., Kuzyakov, Y., Delgado-Baquerizo,
- 462 M., Bastida, F., 2022. Priming effects in soils across Europe. Global Change Biol., 1-12.
- 463 https://doi.org/10.1111/gcb.16062.
- 464 Sistla, S.A., Schimel, J.P., 2012. Stoichiometric flexibility as a regulator of carbon and nutrient cycling
- 465 in terrestrial ecosystems under change. New Phytol. 196, 68-78.
- 466 <u>https://doi.org/10.1111/j.1469-8137.2012.04234.x.</u>
- 467 Soong, J.L., Marañon-Jimenez, S., Cotrufo, M.F., Boeckx, P., Bod & S., Guenet, B., Peñuelas, J.,
- 468 Richter, A., Stahl, C., Verbruggen, E., Janssens, I.A., 2018. Soil microbial CNP and respiration
- 469 responses to organic matter and nutrient additions: Evidence from a tropical soil incubation. Soil
- 470 Biol. Biochem. 122, 141-149. https://doi.org/10.1016/j.soilbio.2018.04.011.
- 471 Tei, F., De Neve, S., de Haan, J., Kristensen, H.L., 2020. Nitrogen management of vegetable crops. Agr.
- 472 Water Manage. 240. https://doi.org/10.1016/j.agwat.2020.106316.
- 473 Wang, C., Wang, X., Liu, D., Wu, H., Lu, X., Fang, Y., Cheng, W., Luo, W., Jiang, P., Shi, J., Yin, H.,
- 474 Zhou, J., Han, X., Bai, E., 2014. Aridity threshold in controlling ecosystem nitrogen cycling in arid
- and semi-arid grasslands. Nat. Commun. 5, 4799. https://doi.org/10.1038/ncomms5799.
- Wang, X.G., Lü, X.T., Zhang, H.Y., Dijkstra, F.A., Jiang, Y.G., Wang, X.B., Lu, J.Y., Wu, Y., Wang,
- 477 Z.W., Han, X.G., 2020. Changes in soil C:N:P stoichiometry along an aridity gradient in drylands of
- 478 northern China. Geoderma 361, 114087. https://doi.org/10.1016/j.geoderma.2019.114087.
- 479 Wei, X., Zhu, Z., Liu, Y., Luo, Y., Deng, Y., Xu, X., Liu, S., Richter, A., Shibistova, O., Guggenberger,
- 480 G., 2020. C:N:P stoichiometry regulates soil organic carbon mineralization and concomitant shifts in
- 481 microbial community composition in paddy soil. Biol. Fert. Soils. 56, 1093-1107.
- 482 <u>https://doi.org/10.1007/s00374-020-01468-7.</u>





483	Wei, X.M., Hu, Y.J., Razavi, B.S., Zhou, J., Shen, J.L., Nannipieri, P., Wu, J.S., Ge, T.D., 2019. Rare
484	taxa of alkaline phosphomonoesterase-harboring microorganisms mediate soil phosphorus
485	mineralization. Soil Biol. Biochem. 131, 62-70. https://doi.org/10.1016/j.soilbio.2018.12.025.
486	Xu, H., Cai, A.D., Wu, D., Liang, G.P., Xiao, J., Xu, M.G., Colinet, G., Zhang, W.J., 2021. Effects of
487	biochar application on crop productivity, soil carbon sequestration, and global warming potential
488	controlled by biochar C:N ratio and soil pH: A global meta-analysis. Soil Till. Res. 213, 105125.
489	https://doi.org/10.1016/j.still.2021.105125.
490	Yu, Z.P., Wang, M.H., Huang, Z.Q., Lin, T.C., Vadeboncoeur, M.A., Searle, E.B., Chen, H.Y.H., 2018.
491	Temporal changes in soil C-N-P stoichiometry over the past 60 years across subtropical China.
492	Global Change Biol. 24, 1308-1320. https://doi.org/10.1111/gcb.13939.
493	Yue, K., Fornara, D.A., Yang, W., Peng, Y., Li, Z., Wu, F., Peng, C., 2017. Effects of three global
494	change drivers on terrestrial C:N:P stoichiometry: a global synthesis. Global Change Biol. 23,
495	2450-2463. https://doi.org/10.1111/gcb.13569.
496	Zhu, Z.K., Ge, T.D., Luo, Y., Liu, S.L., Xu, X.L., Tong, C.L., Shibistova, O., Guggenberger, G., Wu,
497	J.S., 2018. Microbial stoichiometric flexibility regulates rice straw mineralization and its priming
498	effect in paddy soil. Soil Biol. Biochem. 121, 67-76. https://doi.org/10.1016/j.soilbio.2018.03.003.
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501 Figure captions: 502 Fig. 1 The ratio of soil C:N (a), C:P (b), and N:P (c) and microbial C:N (d), C:P (e), and N:P (f) under 503 rhizosphere and bulk soil. The boxes show the 25 % and 75 % percentiles, and the lines in the boxes 504 represent the medians. Different letters indicate significant difference at P < 0.05. 505 Fig. 2 Rhizospheric effects (%) on soil and microbial C:N, C:P, and N:P ratios. Dots and bars represent 506 mean and 95% confidence intervals of rhizospheric effects. Black and red represent rhizospheric effects 507 on soil and microbial stoichiometry, respectively. Vertical dashed lines indicate non-significant effects. 508 Rhizospheric effects are statistically significant if the 95% confidence intervals do not overlap with the 509 vertical dashed lines. Values in parentheses represent sample sizes. 510 Fig. 3 Rhizospheric effects (%) on soil (a) microbial (b) C:N ratios for various climate zones and 511 aridity indexes. Dots and bars represent mean and 95% confidence intervals of rhizospheric effects. 512 Black and red represent rhizospheric effects on soil and microbial stoichiometry, respectively. The 513 vertical dashed lines indicate non-significant effects. Rhizospheric effects are statistically significant if 514 the 95% confidence intervals do not overlap with the vertical dashed lines. Values in parentheses 515 represent the sample sizes. Fig. 4 Rhizospheric effects (%) on soil (a) microbial (b) C:N ratios under various soil pH, soil organic 516 517 carbon (SOC, g kg⁻¹), and soil ammonium nitrogen (NH₄⁺-N, mg kg⁻¹). Dots and bars represent mean 518 and 95% confidence intervals of rhizosphere effects. Black and red represent rhizospheric effects on 519 soil and microbial stoichiometry, respectively. Vertical dashed lines indicate non-significant effects. 520 Rhizospheric effects are statistically significant if the 95% confidence intervals do not overlap with the 521 vertical dashed lines. Values in parentheses represent sample sizes. 522 Fig. 5 Rhizospheric effects (%) on soil (a) microbial (b) C:N ratios under various crop types. Dots and 523 bars represent mean and 95% confidence intervals of rhizospheric effects. Black and red represent 524 rhizospheric effects on soil and microbial stoichiometry, respectively. Vertical dashed lines indicate the 525 non-significant effects. Rhizospheric effects are statistically significant if the 95% confidence intervals 526 do not overlap with the vertical dashed lines. Values in parentheses represent sample sizes. 527 Fig. 6 The relative influence (%) of environmental variables for boosted regression tree model on 528 rhizospheric soil (a) and microbial (b) C:N ratio. The variables include crop types, aridity index (AI), 529 and rhizospheric effects of soil organic carbon (SOC), soil pH, soil total phosphorous (TP), soil 530 available phosphorous (AP), soil nitrate-nitrogen (NO₃-N), and soil ammonium nitrogen (NH₄⁺-N).

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531 Fig. 7 Relationships between C:N:P stoichiometry response ratios of soil and microbial. The blue lines 532 indicate the slopes from the linear mixed-effects models, and the red shadings represent the 95% 533 confidence intervals. N in the figure represents the number of observations. 534 Fig. 8 Mechanisms of rhizospheric effects on soil and microbial stoichiometry. Values presented were obtained from the meta-analysis in this study, where '+' and '-' denote increased and decreased 535 536 responses to rhizospheric effects. Red and blue lines represent positive and negative correlations, 537 respectively. The thicknesses of lines represent the magnitude of correlation coefficients, and dashed 538 lines represent no correlation. SOC: soil organic carbon. NH₄+-N: Ammonium nitrogen.





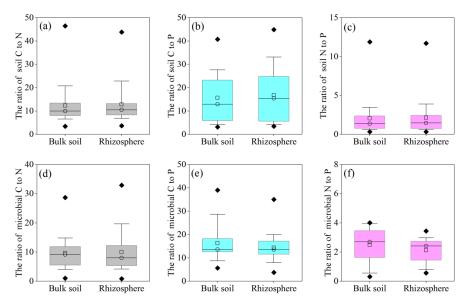


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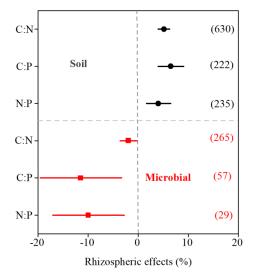
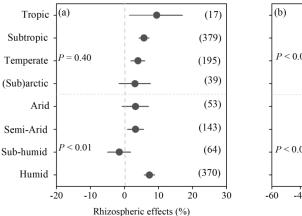
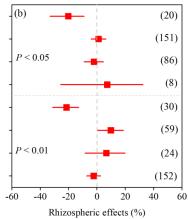


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Fig. 3 Rhizospheric effects (%) on soil (a) microbial (b) C:N ratios for various climate zones and aridity indexes. Dots and bars represent mean and 95% confidence intervals of rhizospheric effects. Black and red represent rhizospheric effects on soil and microbial stoichiometry, respectively. The vertical dashed lines indicate non-significant effects. Rhizospheric effects are statistically significant if the 95% confidence intervals do not overlap with the vertical dashed lines. Values in parentheses represent the sample sizes.





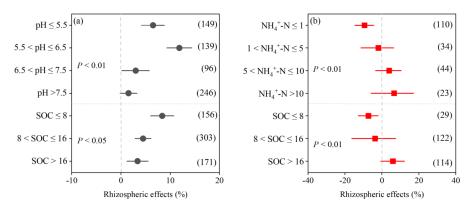
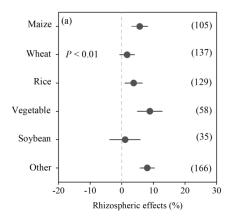


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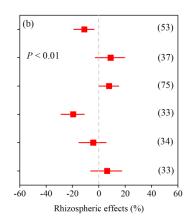


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(b)

 $R^2 = 0.75$

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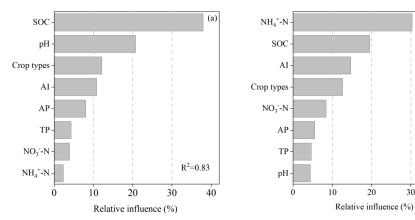


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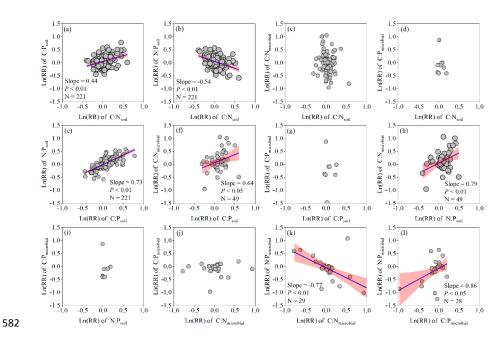


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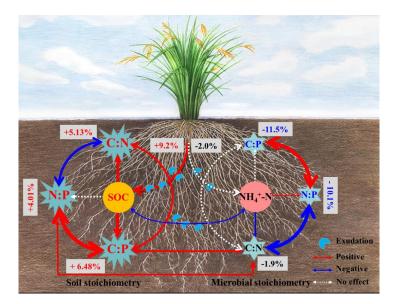


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