





# The abundant fraction of soil microbiomes regulates the rhizosphere function in crop wild progenitors

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## Abstract

The rhizosphere influence on the soil microbiome and function of crop wild progenitors (CWPs) remains virtually unknown, despite its relevance to develop microbiome-oriented tools in sustainable agriculture. Here, we quantified the rhizosphere influence—a comparison between rhizosphere and bulk soil samples—on bacterial, fungal, protists and invertebrate communities and on soil multifunctionality across nine CWPs at their sites of origin. Overall, rhizosphere influence was higher for abundant taxa across the four microbial groups and had a positive influence on rhizosphere soil organic C and nutrient contents compared to bulk soils. The rhizosphere influence on abundant soil microbiomes was more important for soil multifunctionality than rare taxa and environmental conditions. Our results are a starting point towards the use of CWPs for rhizosphere engineering in modern crops.

## KEY WORDS

abundant and rare taxa, crop wild progenitors, plant domestication, plant–soil interactions, rhizosphere, soil biodiversity, soil multifunctionality

## INTRODUCTION

Soil biodiversity is pivotal in promoting multiple soil functions (Bradford et al., 2014; Delgado-Baquerizo et al., 2016; Wagg et al., 2014). Multiple elements of soil biodiversity maintain ecosystem functioning, with abundant and rare taxa playing

different roles (Zhang et al., 2022) and various groups of soil organisms contributing to particular functions (Delgado-Baquerizo et al., 2020). While the mass-ratio hypothesis predicts that abundant species govern ecosystem functioning (Grime, 1998), rare biota could play an over-proportional role despite their low abundance when considering multiple functions, i.e.,

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multifunctionality (Chen et al., 2020; Le Bagousse-Pinguet et al., 2019; Wang et al., 2023). In soil ecosystems, generalist functions such as organic matter degradation and nutrient cycling are performed by multiple soil taxa, while specific functions such as pathogen control or plant–soil mutualism may be associated with particular taxa (Crowther et al., 2019). However, the joint contribution of the abundant and rare fractions of different soil organisms to soil multifunctionality remains poorly understood.

The interaction between plants and soil biota takes place fundamentally in the rhizosphere, defined as the soil intimately associated with roots (Otten, 2008). As such, the rhizosphere can influence microbial communities and functions compared with surrounding bulk soils, as this compartment offers a complex niche for soil organisms, with a strong impact on plant nutrition and growth (Kumawat et al., 2022). Plant–soil biota interactions within the rhizosphere support several functions, including nutrient acquisition, carbon cycling, pathogen control, or mutualism (Jiao et al., 2022; Ling et al., 2022; Marasco et al., 2018; Nannipieri et al., 2003). In agricultural soils, microbiome engineering practices harnessing the rhizosphere influence on microbiomes and functions are expected to enhance crop yields and resilience while reducing the need for external inputs (Arif et al., 2020). For instance, microbial biostimulants and biofertilizers can further modify the composition and functioning of rhizosphere microbiomes by influencing soil conditions and microbial community dynamics (Schmidt et al., 2019; Xie et al., 2022). However, the evolution of crops under domestication has led to unintended changes in plant traits, that were accompanied by changes in land management (Milla et al., 2015). This would result in the disruption of plant-microbial interactions that compromise the rhizosphere influence (Liu et al., 2019; Martín-Robles et al., 2018; Pérez-Jaramillo et al., 2016) and obscure a mechanistic understanding of its effects on plants and ecosystem functioning.

Crop wild progenitors (CWPs) have been used as genetic resources to improve crop growth and health (Renzi et al., 2022). In addition, the beneficial interactions of CWP with soil biota and their impacts on soil functionality could be leveraged to develop microbiome-oriented tools for sustainable agriculture (Pérez-Jaramillo et al., 2016). While previous research has explored the rhizosphere of CWPs, these manipulative studies often focused on single crop species under controlled conditions, such as greenhouses or common gardens (da Silva et al., 2023; Leff et al., 2017; Lund et al., 2022; Pérez-Jaramillo et al., 2019). No study to date has systematically investigated the rhizosphere of multiple CWPs at their native sites of origin. Additionally, no study has evaluated the relevance of plant–soil biota (abundant and rare) interactions in delivering rhizosphere functions and how the environmental gradients across their native distribution could affect these interactions.

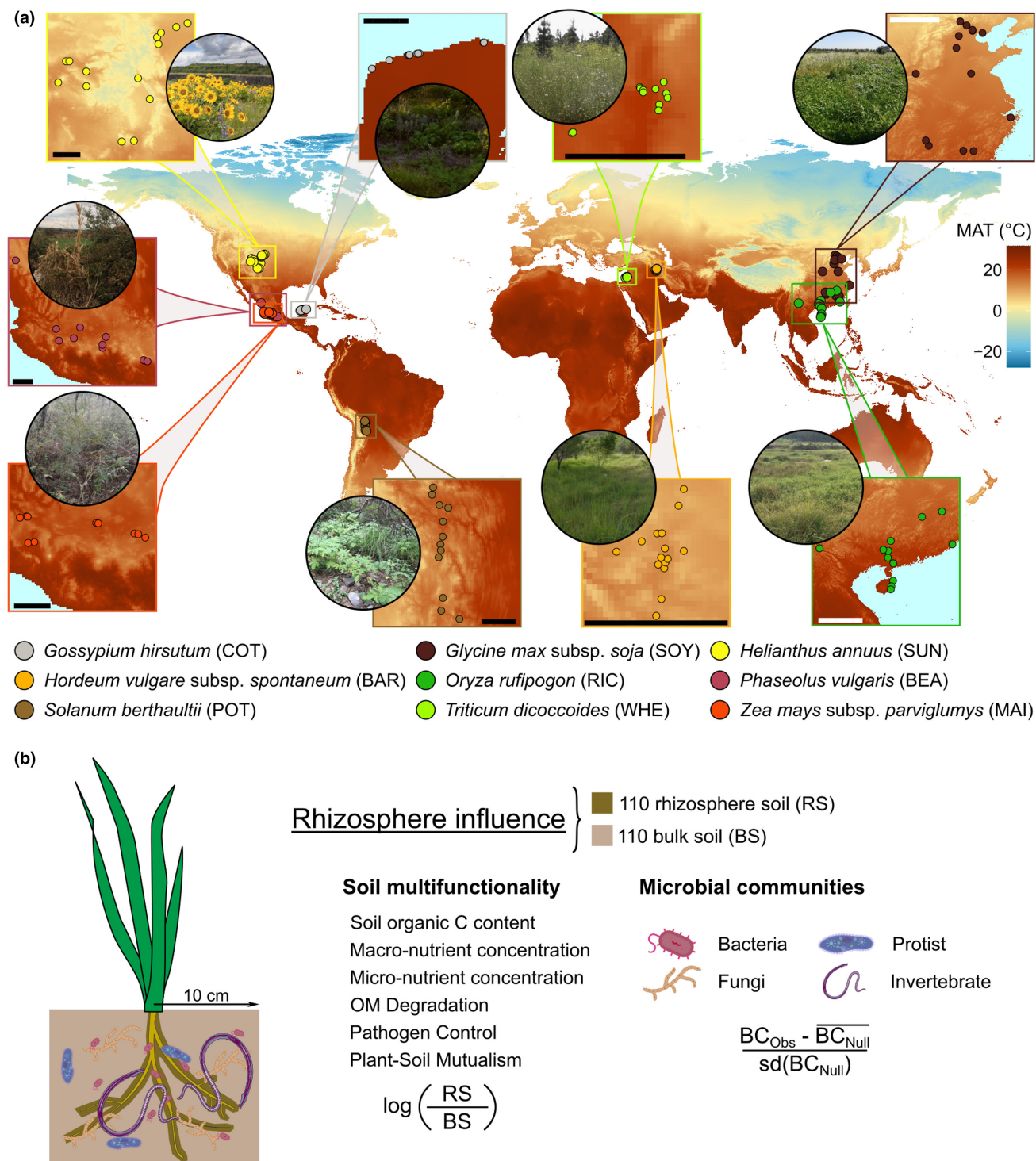
Here, we quantified the rhizosphere influence on soil biota and multifunctionality across the wild progenitors of nine crops, namely: rice, maize, wheat, barley, common bean, soya, potato, sunflower and cotton (Table S1), which together comprise ca. 60% of the cultivated area globally (FAOSTAT, 2023). We conducted a comprehensive sampling of rhizosphere and bulk soils from 110 wild populations along the geographic distributions of these nine CWPs, including ecologically broad edaphoclimatic gradients that span deserts to tropical seasonal forests and savannas (Fernández-Alonso et al., 2023) (Figure 1). We studied four microbial groups: bacteria, fungi, protist and invertebrate communities and measured 20 soil metrics including soil organic carbon content, nutrient cycling, pathogen control, plant–soil mutualisms and organic matter degradation. First, we analysed the rhizosphere influence on soil biotas and functions across CWPs. Then, we assessed the relationship between changes in rhizosphere communities and multifunctionality, distinguishing the effects of abundant and rare taxa, while controlling for environmental drivers.

## MATERIALS AND METHODS

We investigated the links between microbiome (abundant and rare) and soil functionality in the rhizosphere of nine CWPs. First, we conducted a comparative analysis of bacterial, fungal, protists and invertebrate communities among CWPs in their native habitats and further evaluated the rhizosphere influence on microbial communities by means of abundance-based null models used to quantify the compositional disparities between rhizosphere and bulk soils. Then, we assessed soil functionality (measuring 20 soil metrics related to carbon sequestration, nutrient cycling, pathogen control, plant–soil mutualism and OM degradation) across CWPs, using the log-scaled response ratio between soil compartments (rhizosphere and bulk soils) to evaluate the rhizosphere influence on each function. Finally, we assessed the relationship between the rhizosphere influence on microbial communities (disaggregating abundant and rare taxa) and soil multifunctionality.

### Study species and sites

We selected the most probable wild progenitor of nine major crops (Supplementary methods, Table S4), taking ca. 61% of the total harvested area and ca. 40% of the global crop production between 2012 and 2021 (queried on 3 January 2023, FAOSTAT – <https://www.fao.org/faostat>). We sampled 10 to 15 sites per wild progenitor (specific site numbers shown in Table S4) following environmental gradients (e.g., along elevation or latitude) across their native range of distribution. Sampling was designed to maximize environmental variation across



**FIGURE 1** Global survey to investigate rhizosphere influence of crop wild progenitors on soil functions and communities. (a) Locations of the 110 sites surveyed in the centers of origin of wild progenitors. Black scale bars represent 100 km while white bars represent 500 km distance. (b) Schematic representation of rhizosphere influences based on bulk soil (BS) and rhizosphere (RS) measurements. Rhizosphere influence on soil functions was calculated as a response ratio: log scaled ratio of soil functions in the RS compared to the BS. Rhizosphere influence on microbial communities was calculated using abundance-based null models quantifying the compositional disparities between soil compartments. Compositional disparities were calculated as the standardized effect size of observed Bray–Curtis dissimilarity between paired bulk and rhizosphere communities ( $BC_{Obs}$ ) and null dissimilarities ( $BC_{Null}$ ).

sites in climatic and soil properties that potentially control soil microbiomes. Between 2020 and 2021, we sampled 110 sites across four continents from deserts

to tropical forests and savannas. Climatic conditions spanned from 5.3 to 26.4°C MAT, 221 to 1998 mm MAP, 4.4 to 9.0 soil pH and 6.7% to 91.0% sand content

(Figure 1; Table S5; Supplementary File S1). Sites from the same wild progenitor were at least 1 km apart from each other (1–1623 km) and with little sign of human disturbances such as fires, grazing and agriculture. At each site we established a 20×20 m plot and selected five plant individuals, separated at least by 5 m, at a similar phenological stage (flowering) and recorded their geographical locations (latitude, longitude and elevation, Supplementary File S1). The climatic variables used were the mean annual temperature (MAT), temperature seasonality (TSEA) and the mean annual precipitation (MAP) and were obtained for each site from WorldClim (<http://www.worldclim.org>) at a resolution of 1 km. We did not consider precipitation seasonality because it strongly increased the variance inflation factor (VIF > 30).

### Rhizosphere influence on microbial communities and multifunctionality

We collected soils from under individual plants, under their area of influence, bulk and in close contact with roots, rhizosphere (Supplementary methods). This sampling design allows us to evaluate the effects exerted by plants over soils by addressing potential changes between bulk and rhizosphere (Ramirez et al., 2019). We used bulk and rhizosphere samples to calculate the rhizosphere influence on microbial communities and multiple soil functions (Figure 1). In total, we collected 110 bulk soil samples and 110 rhizosphere soil samples. All soil samples were sieved at 2 mm and stored at 4°C until shipment to Universidad Rey Juan Carlos (URJC, Madrid, Spain). At URJC, each bulk and rhizosphere soil samples were separated in two portions (Supplementary methods). We analysed a total of 220 soil samples and calculated site-level estimates of soil biodiversity and soil functions as explained below. Soil pH and texture were measured for the bulk soil samples. Soil pH was analysed in deionized water extracts (suspension ratio of 1:2.5 weight:volume). Soil texture (percentage of sand) was determined using the Bouyoucos hydrometer method.

### Amplicon sequencing

Soil DNA was extracted at URJC using the DNeasy PowerSoil Kit (Qiagen) following manufacturer's instructions (Supplementary methods). The diversity and community structure of soil bacteria, fungi, protists and invertebrates were determined by amplicon sequencing. Library preparation and amplicon sequencing were carried out at the Next Generation Sequencing Facility (Western Sydney University, Australia) using different primer sets for each microbial group studied (Supplementary methods). Libraries were subsequently

sequenced on Illumina® MiSeq instrument as per the manufacturer's instructions.

Bioinformatic analyses were conducted to obtain high-quality chimera-free bacterial, fungal, protist and invertebrate sequences (Supplementary methods). Representative sequences were annotated with QIIME2 v2022.11 (Bolyen et al., 2019) against UNITE v9.0 (Nilsson et al., 2019) for ITS data and SILVA v138 database (Quast et al., 2012) for 16S and 18S data. A normalization procedure was performed at 12000, 8000, 1500 and 250 reads per sample (for bacteria, fungi, protist and invertebrate) and those with less reads were not included in the downstream analysis (Figure S1).

### Soil functions and multifunctionality

We measured a set of 20 soil variables in each of the 220 bulk and rhizosphere soil samples related to soil functions such as nutrient cycling, biological productivity, mineral content and the buildup of carbon and nutrient pools (Maestre et al., 2022). Total nitrogen (N) and total organic C content were determined using an Elemental Analyser (C/N Flash EA 112 Series-Leco Truspec). Available P (in the form of  $\text{PO}_4^-$ ) was determined by ionic chromatography with a liquid chromatograph (Metrohm, Switzerland). Ca, Mg, Cu, Mn, Zn, K and Fe were extracted using wet acid digestion and their concentrations determined using inductively coupled plasma optical emission spectrometry (Varian 720-ES ICP-OES). We also determined the potential activity ( $\text{nmol activity g}^{-1} \text{ dw soil h}^{-1}$ ) of eight extracellular enzymes  $\beta$ -1,4-glucosidase (BG),  $\alpha$ -1,4-glucosidase (AG),  $\beta$ -D-cellobiohydrolase (CB), xylanase (XYL),  $\beta$ -1,4-N-acetylglucosaminidase (NAG), LAP (L-leucine aminopeptidase), PHOS (acid phosphatase) and arylsulfatase (AS), related to C (BG, AG, CB and XYL), N (NAG and LAP), P (PHOS) and S (AS) cycling using fluorometry and 4-methylumbelliferone and 7-amino-4-methylcoumarin to produce the standard curves (Bell et al., 2013).

We grouped the measured soil variables into six broader soil functions. We used soil organic C content (%) to measure the buildup of the soil C pool. When comparing among globally distributed sites, the content of soil organic C can be interpreted as a soil function assessing the potential of the soil C pool to drive land C-climate feedbacks (García-Palacios et al., 2021; Maestre et al., 2022). We used total nitrogen (TN), P, Ca and Mg concentrations as proxies of soil macronutrients (Maathuis, 2009) and Cu, Mn, Zn, K and Fe of micro-nutrients (Lombi et al., 2011). The potential activity of the eight extracellular enzymes were used as indicators of soil organic matter degradation (Sinsabaugh et al., 2008). Besides, we also considered pathogen control and plant soil-mutualism as broad soil functions (Fan et al., 2023) and quantified them using the relative proportion of zOTUs from potential

fungal plant pathogens and mycorrhizal fungi obtained using the FungalTraits v1.2 database (Pöhlme et al., 2020).

We used multifunctionality to summarize the potential of bulk and rhizosphere soils to deliver multiple soil functions simultaneously (Manning et al., 2018). The averaging multifunctionality metric allows to assess whether the average level of multiple functions increase in the rhizosphere, compared to bulk soils. Then we assessed whether rhizosphere-bulk soil differences could be related to changes in microbial community composition, while accounting for the identity of the wild progenitor sampled (Byrnes et al., 2014; Maestre et al., 2012). Multifunctionality was computed as follows. We first standardized the 20 individual variables between 0 and 1 using a min–max normalization. Then, we averaged the measures of each soil function category and finally we averaged them again to calculate a soil multifunctionality index (Delgado-Baquerizo et al., 2020). To check if our results are dependent on the multifunctionality index used, we confirmed our results with the multi-threshold approach and principal coordinate analysis (PCA) (Supplementary methods).

## Statistical analyses

### Rhizosphere influence on microbial communities

We first addressed differences in the  $\beta$ -diversity of bacterial, fungal, protist and invertebrate communities among CWP and between rhizosphere and bulk soil compartments. To this end, we calculated the Bray–Curtis dissimilarities to reflect the variance in community composition and performed nested multivariate permutational multivariate analysis of variance (PERMANOVA). Soil compartment and CWP identity were used as fixed factors and the identities of sampling sites as random factors (to account for the paired sampling design). We visualized  $\beta$ -diversities using non-metric multidimensional scaling (NMDS). These analyses were conducted using the *vegdist* and *adonis2* (999 permutations and the *strata* term) from the *vegan* v2.6-6.1 R package (Oksanen et al., 2022). Besides, we applied variance partitioning analysis on Bray–Curtis dissimilarity matrices, using the *varpart* function from the *vegan* R package (Oksanen et al., 2022), to assess the relative influence of location and host identity in shaping community composition.

Then, we used an abundance-based null model index to evaluate whether compositional differences between paired rhizosphere and bulk soil microbial communities reveal rhizosphere influences on community assembly (Supplementary methods). As abundant and rare taxa are thought to be influenced by different ecological processes (Grime, 1998; Jiao et al., 2017; Soliveres

et al., 2016), we evaluated the rhizosphere influence on microbial communities of abundant and rare taxa separately. For each CWP, we classified zOTUs as abundant if their mean abundance was higher than 1%, while those with lower mean abundances were defined as rare (Alonso-Sáez et al., 2015). We used *tNST* function within the *NST* v3.1.10 package and Wilcoxon test to compare values against zero (Ning et al., 2019). This metric allows us to assess the dominant ecological process shaping patterns of compositional disparity between bulk soil and rhizosphere microbial communities under the same regional pool (Ning et al., 2019) and the strength of rhizosphere filtering processes. Positive values represent that microbial communities are more different between compartments than expected by chance, which is consistent with community assembly being governed by rhizosphere influences such as rhizosphere filtering or the selection of specific taxa through root exudates (Vannette & Fukami, 2017; Wang et al., 2022). Negative values indicate that rhizosphere and bulk microbial communities are more similar than expected by chance, as community assembly may be governed by homogenizing processes (Zhang et al., 2020), indicating a low rhizosphere effect on microbial communities.

We further used the ALDEx2 tool, indicator value index and linear mixed models to determine differences at phylum and zOTU levels in terms of relative abundance between paired rhizosphere and bulk soil samples and indicator taxa analysis to identify zOTUs significantly associated with the rhizosphere (Supplementary methods).

### Rhizosphere influence on multifunctionality

To evaluate the differences in soil functioning among CWP and between soil compartments we used PCA and scaled variables (*scale* R function) so that mean values are 0 and standard deviations 1 (Supplementary methods). In addition, we used variance partitioning analysis to assess the relative influence of location as compared to host identity in shaping soil functionality (Supplementary methods). To quantify the magnitude of the rhizosphere influence on soil functions, we calculated the log-based ratio for each function by dividing the rhizosphere value by the corresponding bulk soil value.

### Relationship between rhizosphere influence on microbial communities and multifunctionality

To address whether rhizosphere influence on microbial communities cascades into changes in the rhizosphere soil functioning, we used structural equation modelling (SEM). First, we hypothesized a conceptual causal model focusing on the abundant and rare taxa separately (Figure S10). Not

only abundant and rare taxa might play different roles on soil multifunctionality (Zhang et al., 2022), but also, they might have different sensitivities to ecological processes such as dispersal and selection (Jiao et al., 2019). Thus, we hypothesized that studying their associations with host progenitors and soil functions separately will better explain the processes shaping changes in rhizosphere microbial community and function. We accounted for the variation in multiple factors driving rhizosphere effects, such as spatial influence (longitude, latitude and elevation), climate (MAT, TSEA and MAP) and soil properties (pH and sand percentage). We created a composite variable accounting for the strength of rhizosphere influence on bacterial, fungal, protist and invertebrate communities simultaneously, using their estimate coefficients on the rhizosphere influence on multifunctionality. While we acknowledge that other relationships are also plausible (i.e., rhizosphere modification of soil functioning drives soil biodiversity), we focused on the direction of relationships that aligns better with previous observations (Zhang et al., 2022). Information about our a priori model is provided in the Figure S10 and Table S6. We used *piecewiseSEM* v2.3.0 (Lefcheck, 2016) and *nlme* v3.1-160 (Pinheiro & Bates, 2023) R packages, which accounts for the random effects derived from the experimental design and provides ‘marginal’ and ‘conditional’ explained variances. We calculated a linear mixed model for each endogenous variable in the model, with the identity of wild progenitor as random factor and the exogenous variables represented in the a priori model as fixed factors. Then, we used the *psem* function to unite all the structural equations into a single structural equation model. The goodness of fit was assessed with the Fisher's *C*-test, to test if the model is a causal scenario consistent with the data ( $p$ -value >0.05).

## RESULTS

### Rhizosphere influence on microbial communities

The composition of bacterial, fungal, protist and invertebrate communities differed among the nine CWPs surveyed at their natural sites of origin, with host identity explaining more variance among bacterial than eukaryote communities (Figure S2; Table S1). We also found that microbial community composition differed between bulk soils and rhizospheres across the four microbial groups (Table S1). This difference was also relevant at the phylum level, with *Actinobacteria* and *Proteobacteria* bacterial phyla enriched in the rhizosphere, while the invertebrate phylum *Nematoda* was filtered out (Figure S3). In fact, differences in bacterial and invertebrate community composition between rhizosphere and bulk soil were higher in non-cereal than in cereal CWPs (Wilcoxon test,  $p < 0.05$ ; Figure S4A).

Both soil compartments presented different taxonomic composition in abundant and rare taxa (Figure S5). As

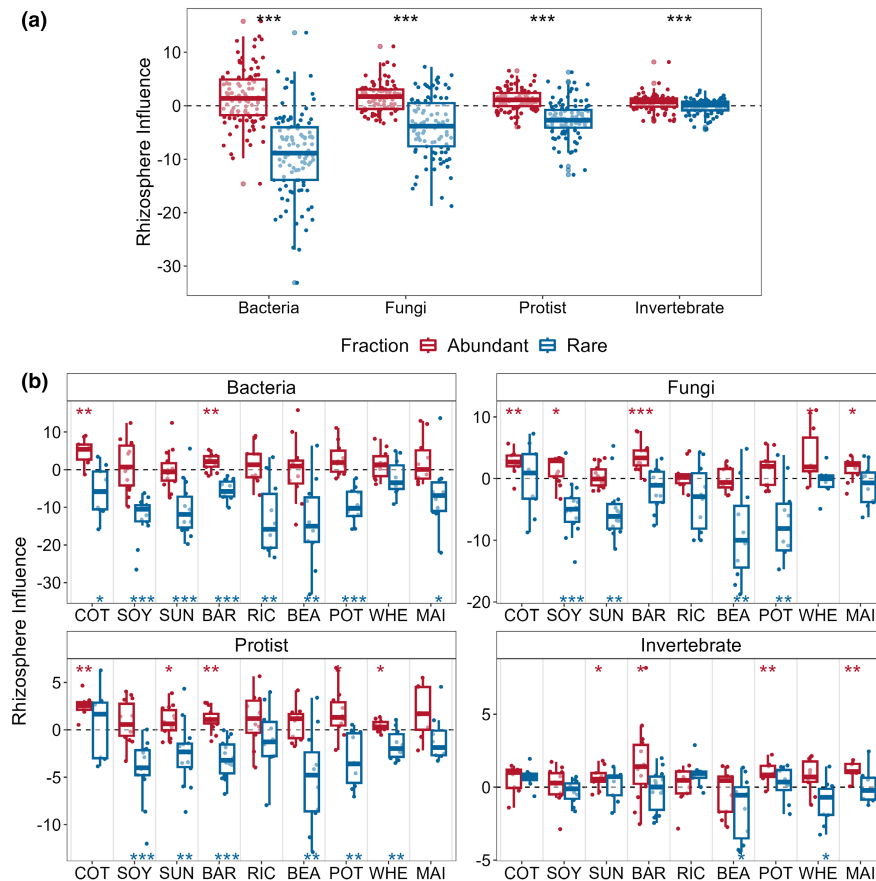
such, rhizosphere influence, quantified as the compositional disparity between rhizosphere and bulk soil microbial communities in a null-model, was consistently higher on abundant (i.e. positive) than on rare (i.e. negative) taxa across the four groups (Wilcoxon test,  $p < 0.001$ ; Figure 2a). A closer inspection of this pattern, however, also showed some differences among the four groups and CWP identity (Figure 2b). For instance, wild progenitors of barley (BAR), cotton (COT), sunflower (SUN), potato (POT), wheat (WHE) and maize (MAI) showed positive rhizosphere influence on abundant taxa of at least two soil biodiversity groups and most CWPs had a negative rhizosphere influence on rare taxa. The rhizosphere enriched abundant taxa, mainly bacteria, also varied among CWPs (Figure S6).

### Rhizosphere influence on soil multifunctionality

Soil functions varied among CWPs and, to a lesser extent, between bulk soils and rhizospheres (Figure S7A,B; Table S2). These variations were more pronounced in progenitors of non-cereal crops such as cotton (COT) and sunflower (SUN) than in progenitors of cereal crops (Figure S4B; Table S2). Across CWPs, soil organic C content and micro- and macro-nutrient content increased in the rhizosphere compared to the bulk soils, whereas the enzymatic activity involved in organic matter (OM) degradation decreased (Wilcoxon test,  $p < 0.05$ ; Figure 3a). We did not observe any effect of rhizospheres on pathogen control and plant–soil mutualism. The magnitude of the rhizosphere influence on soil functions was host-specific (Figure S7B). The wild progenitors of cotton (COT), potato (POT) and maize (MAI) exhibited notable increases in rhizosphere soil organic C content and nutrient levels, while sunflower (SUN), rice (RIC) and potato (POT) presented reduction in OM degradation. In turn, the rhizosphere influence on multifunctionality differed among CWP (Figure 3b). Wild progenitors of barley (BAR) and maize (MAI), both cereal crops, significantly increased soil multifunctionality in their rhizospheres compared to bulk soils, while progenitors of non-cereal crops like sunflower (SUN) and soy (SOY) showed a significant decrease. Indeed, wild progenitors of cereal crops showed higher rhizosphere influence on soil multifunctionality, than non-cereal progenitors (Wilcoxon test,  $p < 0.05$ ; Figure S4C).

### Relationship between rhizosphere influence on microbial communities and multifunctionality

We found positive relationships between rhizosphere influence on abundant taxa and multifunctionality after accounting for the rhizosphere influence on microbial communities of rare taxa and key ecosystem factors such as geographic location, climate and soil properties (Figure 4).



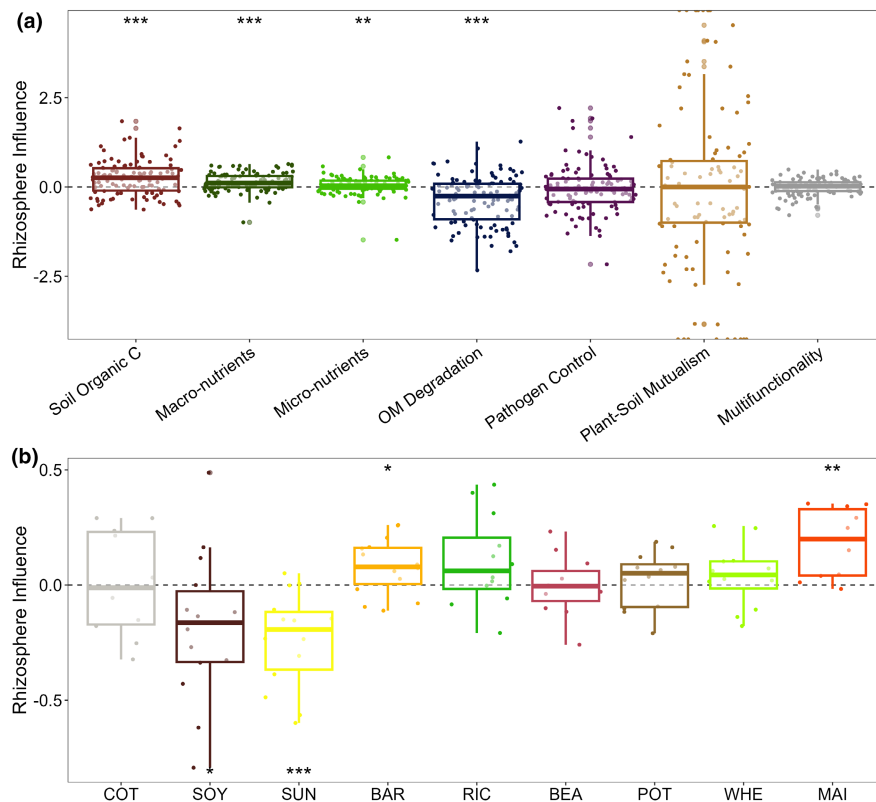
**FIGURE 2** Rhizosphere influence on abundant and rare soil taxa. Rhizosphere influence was measured using an abundance-based null model metric quantifying the compositional disparities between bulk soil and rhizosphere communities. Positive values reveal the importance of rhizosphere filtering effects, while negative values are indicative of high similarity between soil compartments. Red and blue boxplots represent the rhizosphere influence on communities of abundant and rare taxa, respectively. (a) Conserved differences between rhizosphere influence on communities of abundant and rare taxa across progenitors ( $n=110$ ). Asterisks denote significant differences against the null expectation, i.e., 0 (Wilcoxon test for paired samples,  $*p<0.05$ ,  $**p<0.01$ ,  $***p<0.001$ ). (b) Host-specific magnitude of rhizosphere influences revealing filtering on abundant taxa and homogenizing on rare taxa effects ( $n=10-15$ ). Asterisks denote significant differences against the null expectation, i.e., 0 (Wilcoxon test,  $*p<0.05$ ,  $**p<0.01$ ,  $***p<0.001$ ). Initials correspond with wild progenitors as in Figure 1.

Geographic and climate properties modulated the rhizosphere influence on microbial communities of abundant taxa, while soil texture (sand proportion) affected the rhizosphere influence on both abundant and rare taxa. Further, there was a strong correlation between rhizosphere influences on abundant and rare taxa (Figure 4; Table S3). The relatively high proportion of variance explained by random effects (Table S3) suggest the major role of CWPs, in driving the relationships between microbial communities and multifunctionality in the rhizosphere. This is supported by the importance of host identity, rather than sampling location, on shaping rhizosphere multifunctionality and microbial community composition.

## DISCUSSION

The exploration of plant–soil biota interactions, encompassing both abundant and rare taxa, in promoting

multifunctionality within the rhizosphere of CWP remains largely unexplored despite its potential to promote agricultural production and resilience to climate change (De Vries et al., 2020; Pérez-Jaramillo et al., 2016; Raaijmakers & Kiers, 2022). Despite the nine CWPs exhibited distinct microbial community composition, our results revealed consistent rhizosphere influence on both abundant and rare taxa across the nine studied CWPs, with higher values on abundant taxa compared to rare taxa. Rhizospheres increased soil C, micro- and macro-nutrient contents but decreased OM degradation when compared to bulk soils. Rhizosphere influence on soil multifunctionality, taking all functions together, differed among the several CWPs studied. Together our results shed light to the intricate dynamics between plants and soils and revealed the importance of host-specific effects in understanding rhizosphere influence on microbial communities and multifunctionality.



**FIGURE 3** Rhizosphere functionality of crop wild progenitors (CWPs). (a) Rhizosphere influence on multiple soil functions in CWP ( $n = 110$ ), measured as the log scaled proportion of soil functionality and averaging and multifunctionality in the rhizosphere compared to the bulk soils. (b) Host-specific rhizosphere influence on soil multifunctionality. Statistical analysis was performed using Wilcoxon test, asterisk (\*) denote significant differences against 0, which would denote rhizosphere influences, ( $*p < 0.05$ ,  $**p < 0.01$ ,  $***p < 0.001$ );  $n = 10$ – $15$  wild progenitor sites sampled per species. Initials correspond with wild progenitors as in Figure 1.

### Drivers determining the rhizosphere influence on the microbial communities of CWPs

Our study revealed that rhizosphere and bulk soil microbial communities differed consistently more when accounting for abundant taxa compared to rare taxa in bacterial, fungal, protists and invertebrates. While these trends were consistent across all CWPs, the extent of rhizosphere influence on both abundant and rare taxa varied among the studied microbial groups and CWPs. In the rhizosphere, the diversity and composition of microbial communities are influenced by host plants, in addition to soil and climatic variations (Garbeva et al., 2008; Jiang et al., 2017; Liang et al., 2023; Mathesius & Costa, 2021). The stronger rhizosphere influence on bacterial and fungal communities could be caused by plants using root exudates to recruit beneficial bacteria and fungi (Broeckling et al., 2008; Zhalnina et al., 2018), consequently influencing protists and invertebrates feeding on these microbes (Ceja-Navarro et al., 2021). Root morphology and soil aggregation also influence rhizosphere community assembly (Otten, 2008; Whitman et al., 2018). Notably, rhizosheath formation can reduce the ability of cereal plants to influence microbial communities (Mo et al., 2023). This may explain why bacterial

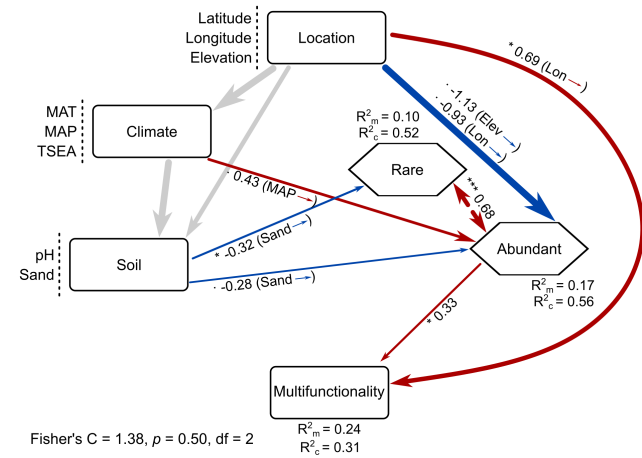
communities differed more in rhizosphere compared to bulk soils non-cereal than in cereal CWPs.

Abundant soil taxa exhibit stronger responses to environmental factors than rare taxa (Liang et al., 2020; Xue et al., 2018; Zhao et al., 2022). This agrees with our observation that abundant taxa are generally more impacted by rhizosphere influence than rare taxa. The negative rhizosphere influence on rare taxa suggests a closer similarity between rhizosphere and bulk soil communities than expected, indicating that rare taxa may be less affected by rhizosphere and bulk soil niche differentiation. Thus, rhizospheres act as effective filters for abundant taxa while exhibiting greater permeability to rare taxa, possibly because of its lower capacity to compete for resource than abundant taxa. This finding contributes to our understanding of the microbial community assemblage in the rhizosphere, emphasizing the need to consider both abundant and rare taxa when evaluating plant–soil interactions.

### Contrasting rhizosphere influences on multifunctionality of CWPs

Similar to the trends observed in soil biotas, rhizosphere influence on specific soil functions remained uniform





**FIGURE 4** Relationships between the rhizosphere influences on soil-abundant and rare-taxa and multifunctionality. The rhizosphere influence on abundant and rare taxa was modelled using composite variables (hexagons), reflecting the overall compositional disparities of bacteria, fungi, protists and invertebrates between bulk soils and rhizospheres. Rectangles are observed variables. Location, climate and soil properties are the joint effects of multiple variables, which were grouped in the same box for graphical simplicity. Parentheses indicate which specific observed variable within a box has a causal effect on a response variable. Arrows represent significant associations and adjacent numbers indicate the standardized coefficient of significant paths ( $*p < 0.05$  and  $\cdot p < 0.1$ ). Red and blue arrows represent positive and negative paths, respectively. Grey arrows represent significant associations between geographic factors and edaphoclimatic conditions, provided in Table S3 for graphical simplicity. The double-headed arrow represents an undirected association. Conditional (c) and marginal (m)  $R^2$  represent the proportion of variance of a response variable explained by all predictors, with and without accounting for the random effect of wild progenitor identity, respectively. Fisher's  $C$  statistic refers to the overall goodness of fit, with a high  $p$  value indicating good fit of the model to the data. MAT, mean annual temperature ( $^{\circ}\text{C}$ ); MAP, mean annual precipitation (mm); TSEA, temperature seasonality (temperature standard deviation  $\times 100$ ); Sand, sand content (%); Elev, elevation (m); Lon, longitude ( $^{\circ}$ ). The rationale behind our a priori model is provided in Figure S10 and Table S6.

across CWPs. Overall, soil C concentration and macro- and micro-nutrient contents increased and OM degradation decreased in the rhizosphere of CWPs. The increase of C content in the rhizosphere could be attributed to the accumulation of root litter and rhizodeposition (Jones et al., 2004; Villarino et al., 2021). Concurrently, nutrient flow from soil to roots powered by transpiration (Chapman et al., 2012; Cramer et al., 2009; Dodd & Lauenroth, 1997) may contribute to the observed enhancement in rhizosphere nutrient content. Some authors have reported negative relationships between N content and rhizosphere OM degradation, linked to increased carbon use efficiency without N limitation (Zang et al., 2016; Zhou et al., 2020). This suggests that the influx of N to rhizospheres would promote lower OM degradation and would result in higher C accumulation.

Despite the consistent patterns found when analysing specific soil functions, the impact of rhizosphere influence on multifunctionality did not exhibit a uniform

trend among progenitors. Cereal progenitors demonstrated increased soil multifunctionality within their rhizospheres, while non-cereal progenitors generally displayed a decrease. This difference could be a consequence of rhizosheath formation observed in cereals, physically enhancing nutrient and water uptake (Galloway et al., 2020). This could explain why despite inducing less changes in rhizosphere communities than non-cereal progenitors, cereals could promote multifunctionality. The lack of a uniform trend in rhizosphere influence on multifunctionality across all CWPs emphasizes the need for a more comprehensive understanding of the diverse strategies employed by different plant species to influence their rhizospheres. Factors such as plant-microbe interactions, root morphology and rhizodeposition dynamics may directly contribute to multifunctionality (Barea et al., 2005; Fry et al., 2018; Trivedi et al., 2020; Villarino et al., 2021). Here, we highlight the importance of considering host-specific effects when evaluating the impact of rhizosphere influence on soil functions and multifunctionality.

### The rhizosphere influence on abundant but not on rare taxa shapes rhizosphere multifunctionality

The positive association between rhizosphere influence on soil biotas and multifunctionality was observed across the four soil biodiversity groups, but this relationship was significant only when considering abundant taxa. Indeed, abundant soil taxa are more associated with individual soil functions than rare taxa (Figure S8). This is in line with the predominant role in shaping and stabilizing soil functionality usually attributed to abundant taxa (Cottrell & David, 2003; Pedrós-Alió, 2012; Xun et al., 2021), given their capacity to occupy diverse niches, effectively adapt to environmental conditions and contribute to the majority of biomass (Barberán et al., 2014; Jousset et al., 2017; Nemergut et al., 2011; Shade & Gilbert, 2015). However, Zhang et al. (2022) highlight the importance of rare species for ecosystem multifunctionality in soils associated with rice and maize. Interestingly, we found a more robust and well-fitted biodiversity-multifunctionality association when considering rare taxa than abundant, specifically in the wild progenitors of maize (MAI) and rice (RIC) (Figure S9). This suggests a unique relationship between these progenitors and their associated functional rhizosphere microbiome, possibly preserved during domestication. Besides, the correlation between rhizosphere influences on abundant and rare taxa highlights the role of biotic interactions in shaping the rhizosphere, a pathway by which rare taxa can affect overall community assembly (Mokany et al., 2013).

Importantly, the linkage between the rhizosphere influence on abundant taxa and multifunctionality persisted even after accounting for the effect of key

ecosystem factors such as location, climate and soil properties. Edaphoclimatic factors that shape the biodiversity-multifunctionality relationship, specifically precipitation and soil texture, are associated with water availability in soils, which alter community assembly processes (Dodd & Lauenroth, 1997; Yang et al., 2022). This agrees with a previous global study that found similar biodiversity-multifunctionality relationships, suggesting a potential influence of soil biotic and climatic factors on this relationship (Delgado-Baquerizo et al., 2020). In addition, several studies have described host-specific influence on soil diversity (Berendsen et al., 2012; Lewin et al., 2021; Zhang et al., 2020), suggesting that plants play a pivotal role in shaping biodiversity-multifunctionality relationships. This host-specificity adds a layer of complexity to the already intricate dynamics between plants and their associated soil communities. Future research endeavours should delve deeper into the specific mechanisms governing the observed patterns, shedding light on the intricate relationship between CWP and their rhizospheres. Understanding these nuances will be crucial for harnessing the full potential of rhizosphere influence in sustainable agriculture and ecosystem functioning.

Our comprehensive observational study across nine CWPs evaluated the rhizosphere influence on microbial communities and multifunctionality, but it is not without limitations. Here, we identify aspects that are not covered in our study and suggest new research avenues to propel future investigations. Although our work represents a baseline for future rewilding comparisons (De Vries et al., 2020), to investigate whether plant domestication has altered the ability of crops to interact with soil organisms, the microbiome of different crops and their wild progenitors should be compared (Pérez-Jaramillo et al., 2016). To do that, both observational comparisons across large environmental gradients and mechanistic experiments where seeds and soils from modern cultivars and wild progenitors are grown in a fully-crossed design are particularly meaningful. Including the measurement of plant traits that determine microbiome colonization and establishment in key plant compartments (i.e. rhizosphere, root endosphere, phyllosphere) will improve assessing the linkages between host identity, microbiome and ecosystem function (Kembel et al., 2014; Lutz et al., 2023). The focus on multifunctionality allows to synthesize many rhizosphere functions that could be influenced by microbial or plant activity into one metric, while it does not account for tradeoffs between functions, which remains a fertile arena for new research.

## CONCLUSIONS

Understanding the relationship between soil organisms and function occurring in the rhizosphere of CWPs

can help to harness agricultural microbiomes (De Vries et al., 2020; Pérez-Jaramillo et al., 2016; Raaijmakers & Kiers, 2022). Despite the distinct soil microbiomes and functions observed across CWPs, rhizosphere influence was, at some extent, consistent among CWPs. Rhizosphere influences were in general stronger on abundant than on rare taxa, presenting significant relationships with rhizosphere multifunctionality. This relationship was further shaped by abiotic environmental conditions as well as by rare biota and the identity of the host progenitor. In essence, our study shows that higher rhizosphere influence on abundant taxa correlates with increased multifunctionality. However, host-specific effects must be considered, as different plant species would employ diverse mechanisms influencing microbial communities and soil functions. This work provides a foundation for exploring microbiomes to target soil functions, with potential applications in rhizosphere engineering for sustainable agriculture.

## AUTHOR CONTRIBUTIONS

P.G.-P., R.M. and M.D.-B. developed the original idea, designed the research and coordinated all field and laboratory operations, with inputs from B.K.S. Field data were collected by L.A.-R., F.D.A., D.A.-P., M.-K.A., J.C., G.-L.D., A.H.-L., K.N., B.P., T.Q.-M., D.S.R., S.S., P.T., Q.Y., Y.Y., E.Z., Y.-G.Z. Data gathering was conducted by M.C., M.J.F.-A. and J.-T.W., with inputs from I.B. Laboratory analyses were carried out by C.G., R.O.-H. and J.P. Data analyses was performed by M.C., M.J.F.-A. and J.-T.W. The manuscript was written by M.C., assisted by M.J.F.-A. and with substantial contributions from all coauthors.

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## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Raw data in support of these findings are openly available in Figshare repository (16S—<https://doi.org/10.6084/m9.figshare.25681107>; 18S—<https://doi.org/10.6084/m9.figshare.25680999>; ITS—<https://doi.org/10.6084/m9.figshare.25681089>). Likewise, code for statistical analyses is available at <https://doi.org/10.6084/m9.figshare.24828954>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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