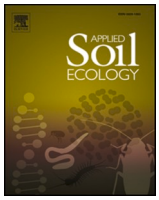
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Research paper

Beneficial fungi as major drivers of root fungal microbiome assembly and network robustness across a soil disturbance gradient

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ABSTRACT

Despite the critical role of soil microbiomes in ecosystem stability, how soil disturbance impacts these communities and their interactions with plants remains poorly understood. In this study, we investigate how different levels of soil disturbance influence the assembly and robustness of the root fungal microbiome. Using a microcosm experiment with tomato plants, we inoculated plants with soil from environments with decreasing levels of disturbance (agricultural field, field margin, and uncultivated field) and tested the variation in composition, assembly process, and network stability of the root fungal microbiome. Results reveal that more disturbed systems, i.e. agricultural soils, harbor fungal microbiomes with less robust networks compared to systems with lower disturbance. Network analysis identified arbuscular mycorrhizal fungi as key taxa contributing to microbiome stability, suggesting their critical role in maintaining the robustness of root-associated fungal microbiomes. Furthermore, stochastic processes dominated fungal community assembly across all soil treatments, yet the key taxa that deviated from null-model predictions include those with a major role in network robustness, and were mainly identified as arbuscular mycorrhizal fungi. Together, our results suggest that arbuscular mycorrhizal fungi are major actors in assembling robust plant microbiomes, and soil disturbance is a key factor in disrupting these interactions.

1. Introduction

Global soils are under the threat of multiple stressors driven by global changes and the intensification of agriculture (Rillig et al., 2023; Phillips et al., 2024). While agricultural activities are essential for the survival and development of our society, intensive agricultural practices produce severe disturbance to soil biological communities (Yang et al., 2021), altering their composition, function, and ultimately impacting whole ecosystems and global health (Banerjee and van der Heijden, 2023). For example, tillage (Angon et al., 2023), synthetic chemicals (Ruuskanen et al., 2023), deforestation (de Souza et al., 2023), climate change (Banerjee and van der Heijden, 2023), and biological invasions (Gao et al., 2022) have been linked to variation in soil microbiome composition and function with negative effects on soil and plant health. Indeed, microbial communities inhabiting soil are key components in maintaining ecosystem functions and stability, with direct impact on plant health and tolerance to environmental stressors (Hartmann and Six, 2023). For example, the effects of fire on the soil microbiome have been linked to reduction in plant productivity (Revillini et al., 2022), and, habitat fragmentation, through soil microbiome-mediated effects, has been found to influence plant performance and resource allocation (Kiesewetter and Afkhami, 2021). However, we still know little about the influence of soil disturbance on the plant microbiome assembly and stability.

The soil microbiome has a major influence on the structure of plant microbiomes, in particular on those associated with belowground compartments (Trivedi et al., 2020; Malacrinò and Bennett, 2024; Mohamed et al., 2024). Environmental stressors, for example drought and increasing temperatures, can have profound effects on the structure and functioning of the soil microbial communities (Jansson and Hofmockel, 2020) and, consequently, of plant microbial communities (Trivedi et al., 2020; Trivedi et al., 2022). Plants under stress can indeed exert a certain degree of selection on their microbiome through the exudation of primary and secondary metabolites (Koprivova and

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Kopriva, 2022; Sasse et al., 2017). These changes can, in turn, improve the ability of plants to forage nutrients and tolerate biotic and abiotic stressors (Rolfe et al., 2019; Pantigoso et al., 2022). Yet, our understanding of how environmental disturbance can alter plant-microbe interactions, and the assembly of the plant microbiome is still limited. While bacteria often dominate studies on soil microbiomes, fungi contribute significantly to nutrient cycling, organic matter decomposition, and plant health (Banerjee and van der Heijden, 2023; Bahram and Netherway, 2022; Fierer et al., 2021). Previous research has indeed shown that different farming systems, with varying levels of soil disturbance, have different effects on the assembly of the root microbial networks (Banerjee et al., 2019). While we have some evidence showing that soil disturbance can disrupt the assembly of plant-associated fungal communities, our understanding of how fungal microbiomes respond to varying levels of soil disturbance, particularly in roots, remains limited.

The assembly of plant-associated microbial communities is influenced by different ecological processes, where both stochasticity and determinism play a role in shaping the final structure of microbiomes at different compartments. However, how this assembly process is altered under different disturbance regimes remains an open question. Under stress, selection by the host plant may play a stronger role in selecting microbial taxa (Barnes et al., 2025; Arnault et al., 2023), favoring beneficial organisms that enhance nutrient acquisition and stress tolerance. For example, beneficial fungi may contribute to the robustness of microbial networks (i.e., the ability to maintain overall structure and connectivity despite the loss or perturbation of individual taxa) by stabilizing plant-fungal interactions and suppressing pathogens (Wang et al., 2024a). On the other hand, soil disturbance could also disrupt plant-microbiome interactions, leading to destabilized networks (Wang et al., 2024b) and promoting stochastic assembly processes, such as drift and dispersal. Understanding the balance between selection and stochasticity, as well as the role of different fungal taxa and functional groups in network stability, is crucial for predicting the consequences of soil disturbance on plant-microbe interactions. At the same time, understanding how microbiomes assemble can provide a solution to mitigate the negative effects of disturbances.

In this study, we asked whether soil disturbance can influence the assembly and the network of interactions within the root-associated fungal communities. We assembled microcosms, inoculated them with soils from sites with varying disturbance levels (agricultural field, field margins, uncultivated field) while controlling for soil abiotic features, and used amplicon sequencing to infer the assembly processes and network of interactions behind the structure of root microbiomes. As observed in our previous studies (Malacrinò and Bennett, 2024; Malacrinò et al., 2021), we predicted an inoculum-specific signature on the root fungal microbiome. We then asked if disturbance influences the ecological processes behind the assembly of the root fungal microbiome and hypothesized that higher levels of disturbance might favor deterministic selection processes, for example by recruiting beneficial organisms, with little contribution from stochastic processes. We also hypothesized that the robustness of the root fungal microbiome network would be influenced by the level of disturbance. Previous studies focusing on the effect of different intensities of agricultural practices on the root fungal microbiome show that microbial networks are more robust in less intensive systems (Banerjee et al., 2019), thus we predict a lower network robustness in plants exposed to the microbial communities derived from the agricultural soil, and a higher robustness in plants grown on microcosms inoculated with soil from the uncultivated field. Finally, we asked whether the fungal taxa supporting the network robustness are specific to each level of disturbance, expecting to observe inoculum-specific fungal taxa involved in both the assembly and robustness of the microbiome network. Considering that we expected a higher influence of deterministic assembly processes, as a consequence of potential microbial recruitment by the host plant, we also predicted that those taxa playing a major role in network robustness would mostly be identified as beneficial fungi.

2. Materials and methods

2.1. Microcosm experiment

We tested our hypotheses by assembling microcosms using soil from sites with different levels of disturbance: an agricultural field, the margins of that field, and an uncultivated field located nearby (Reggio Calabria, Italy). The agricultural field was managed under organic farming and cropped with tomato at the time of sampling as part of a horticultural crop rotation. The field margin consisted of an uncultivated strip bordering the agricultural field and was characterized by spontaneous herbaceous vegetation. The uncultivated field had not been managed for approximately 30 years and supported a more established plant community dominated by perennial grasses and herbaceous plants. At each site, soil was collected between 5 and 15 cm of depth, sieved to 2 cm to remove large debris, homogenized, and stored at 4 °C.

Microcosms were assembled in three groups, one of each inoculum sampled above. Background soil (1:1 v/v mix of sand and soil) was autoclaved at 121 °C for 3 h, allowing it to cool for 24 h, and then autoclaved at 121 °C for a further 3 h. Similarly, a portion of each soil was autoclaved using the same procedure. The soil mix was generated from a mix of all three soils used for inoculation (1:1:1), of which only one was not autoclaved. For example, in the group of microcosms with the alive inoculum from the agricultural soil, each pot (1 L) received a mix of 450 mL of autoclaved background soil, and a mix of 150 mL of alive (non-autoclaved) soil from the agricultural field, 150 mL of autoclaved soil from the field margin, and 150 mL of autoclaved soil from the uncultivated field. Using this approach, soil physicochemical properties were homogenized across treatments to isolate microbial effects from abiotic variation, although we acknowledge that autoclaving soil might have influenced the pool of available nutrients (Berns et al., 2008). Each group of microcosms was replicated over 32 pots, for a total of 96 pots divided into 4 blocks (24 pots of each inoculum per block). Pots were fully randomized between blocks and within each block, accounting for spatial variability of the abiotic environment within the greenhouse. A single tomato seedling (*Solanum lycopersicum* L. variety Moneymaker, previously germinated on autoclaved potting soil) was transplanted to each pot. Plants were then grown in a greenhouse at an average temperature of 25 °C and a photoperiod of 16 h of light and 8 h of darkness. Plants were watered with ~100 mL of tap water three times per week throughout the experiment. Six weeks after the experimental setup, from each pot, we collected ~50 mg of roots from each plant, which were carefully washed with tap water and immediately stored at −80 °C.

2.2. DNA extraction, library preparation, sequencing

Each sample was lysed in an extraction buffer using a bead-mill homogenizer, and total DNA was extracted using a phenol-chloroform protocol. We did not surface sterilize samples, so we characterized both endophyte and epiphyte communities. After quality check, we prepared libraries targeting the fungal ITS region of the rRNA using the primer pair ITS1-ITS2. PCR assays were performed in a total volume of 25 μL, containing approximately 50 ng of DNA, 0.5 μM each primer, 1× KAPA HiFi HotStart ReadyMix (KAPA Biosystems), and nuclease-free water. Amplifications were performed in a Mastercycler Ep Gradient S (Eppendorf) set at 95 °C for 3 min; 98 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s repeated 35 times; and ending with 10 min of extension at 72 °C. Amplifications were also carried out on non-template controls, where the sample was replaced with nuclease-free water to account for possible contamination of instruments, reagents, and consumables used for DNA extraction. After this first PCR, samples were purified (Agencourt AMPure XP kit, Beckman Coulter) and used for a second short-run PCR to ligate Illumina adaptors. Libraries were then purified again, quantified using a Qubit fluorometer (Thermo Fisher Scientific Inc.), normalized using nuclease-free water, pooled together, and sequenced on an Illumina NovaSeq 6000 SP 250PE flow cell at the Genomic

Sciences Laboratory of North Carolina State University (Raleigh, NC, USA).

2.3. Data processing and analysis

Reads were processed with the *nf-core/ampliseq* v2.7.1 pipeline (Straub et al., 2020; Ewels et al., 2020; Di Tommaso et al., 2017) for quality control, adaptor/primer trimming, error correction, clustering of ASVs, chimera removal, and taxonomic identification using the UNITE database v10.0 (Abarenkov et al., 2024). ASV sequences were aligned using *MAFFT* v7.525 (Katoh et al., 2002) and used to build a phylogenetic tree using *FastTree* v2.1.11 (Price et al., 2009). All subsequent data processing and analysis was performed in *R* v4.4.1 (R Core Team, 2020). The ASV table, taxonomic identification table, metadata, and phylogenetic tree were merged using *phyloseq* v1.48 (McMurdie and Holmes, 2013) before subsequent analyses. Likely contaminants were removed using the package *decontam* v1.24 (Davis et al., 2018) and the data from negative control PCRs. Then, singletons and samples with less than 1000 reads were discarded from the dataset. This resulted in a small reduction of replicates for each group ($n = 27$ for agricultural soil, $n = 25$ for field margin, $n = 29$ for uncultivated soil), but still maintaining a high level of replication, and a depth of ~4255 reads/sample, which clustered into 409 ASVs. Data used for calculating relative abundances were normalized using *Wrench* v1.22 (Kumar et al., 2018) before processing.

Differences in microbiome structure were tested using PERMANOVA (999 permutations stratified at the "block" level) and visualized using a NMDS, both performed on a weighted UniFrac distance matrix using the package *vegan* v2.6 (Dixon, 2003). PERMANOVA post-hoc contrasts were performed using the package *RVAideMemoire* v0.9 (Hervé, 2022). The random forest classification was performed using the package *randomForest* v4.7 (Breiman et al., 2002), using the ASV table as predictor and the "soil inoculum" variable as response. The LEfSe (Linear discriminant analysis Effect Size) analysis (Segata et al., 2011) was performed using the package *microeco* v1.13 (Liu et al., 2021). The Shannon diversity index was calculated using the package *microbiome* v1.26 (https://github.com/microbiome/microbiome/), the Faith's phylogenetic diversity, and the MNTD and β-NTI metrics were calculated using the package *picante* v1.8.2 (Kembel et al., 2010) using the "richness" null model. For each univariate metrics, differences between groups were tested by fitting a linear mixed-effect model using the package *lme4* v1.1 (Bates et al., 2015) using the variable "soil inoculum" as fixed factor and the variable "block" as random effect, while post-hoc contrasts were extracted using the package *emmeans* v1.10.7 (Lenth, 2022). The relative contribution of different ecological processes (homogeneous/heterogeneous selection, dispersal limitation, homogenizing dispersal, and ecological drift) in the assembly of the root fungal microbiomes for each soil inoculum was estimated using the package *iCAMP* v1.5.12 (Ning et al., 2020). *iCAMP* infers community assembly mechanisms by first partitioning taxa into phylogenetic bins and then comparing the observed phylogenetic and taxonomic turnover within each bin against null model expectations. Networks were built and analyzed using the package *microeco* v1.13 (Liu et al., 2021) using the Spearman method (thresholds for conserving edges: $\rho > 0.6$ and $p < 0.01$), and used to measure the robustness of microbial network as (i) response of network connectivity to node removal by decreasing degree, and (ii) estimating the Molloy-Reed criterion (Molloy and Reed, 1995) bootstrapped ($n = 1000$) on a subset of each network containing 80% of the nodes from the full network, while maintaining the edges between such nodes. Fit to the Sloan null-model was performed for each soil inoculum using the package *tyRa* v0.1 (https://github.com/DanielSprockett/tyRa).

3. Results

We tested our hypotheses by growing tomato plants in microcosms hosting three different microbial communities, sampled from soils with different levels of disturbance, similarly to our previous work (Malacrinò and Bennett, 2024). The idea is that the agricultural field (cropped with tomato) experienced the highest disturbance due to the conventional agricultural practices, the uncultivated field (undisturbed for the past ~30 years) would bear minimal disturbances, while the field margins (uncultivated area at the border between the uncultivated and the cultivated field) would be at an intermediate level of disturbance between the agricultural and the uncultivated field. Microcosms were assembled by mixing all three soils, of which only one was not autoclaved, thus maintaining alive only the focal biological community (see Methods). This allowed us to control for abiotic factors and focus on the effects driven by the soil microbiomes in the three groups.

Each soil inoculum had a specific effect on the structure of the root fungal community ($F = 8.93$, $R^2 = 0.19$, $p < 0.001$, Fig. 1A), also confirmed by pairwise post-hoc contrasts (FDR-corrected $p < 0.01$ for all combinations). Indeed, looking at the taxonomic composition (Fig. 1B), samples from the agricultural soil treatment were clearly dominated by ASVs identified in the genus *Rhizophagus* (63.3%), those from the field margin had higher abundances of fungi from the genera *Cladosporium* (21.8%) and *Epicoccum* (19.4%), while samples from the uncultivated soil treatment had higher abundances of ASV identified as *Funneliformis* (27.7%) and *Acaulospora* (22.7%). It is important to note that, among the most abundant taxa (Fig. 1B), the root microbiome of all samples includes both potential pathogens (e.g. *Epicoccum*, *Fusarium*) and beneficial organisms (e.g., mycorrhizal fungi from the genera *Acaulospora*, *Funneliformis*, *Rhizophagus*). Additional pathogens, including *Alternaria alternata*, were also identified among the less abundant taxa. Interestingly, the ASVs identified as beneficial organisms were those with the highest discriminatory power among the three soils using both the Random Forest (Fig. 2A) and the LEfSe (Fig. 2B) approaches.

When comparing the diversity of the root fungal communities of plants grown on the different soils, we found no differences between the three groups using Shannon's diversity index (Fig. 3A) and Faith's phylogenetic diversity index (Fig. 3B) as metrics. However, when using the MNTD as a metric, we found a higher diversity in roots grown on the soil from field margin compared to the other two groups (Fig. 3C). We then compared the observed MNTD with a randomly assembled microbiome, using the β-NTI metric, and we found that all three groups had values between 2 and -2 (Fig. 3D), suggesting an assembly dominated by stochastic processes, which was then confirmed by further null-model analyses, showing that in all three groups drift and dispersal contributed more than selection to the assembly of root fungal communities (Fig. 3E).

We then built a correlation network between taxa for each soil inoculum (Fig. 4A-C, Table S1, supplementary materials), showing that the network complexity increased with decreasing disturbance, from agricultural soil, to field margin, and to uncultivated field. Several metrics followed this pattern, including the number of nodes, the average path length, and the network modularity, while others showed that decreasing disturbance generated a less dense and centralized network (Table S1, supplementary materials).

Considering that several network metrics followed the disturbance gradient, we inferred the networks to test their robustness, and identify which taxa might best contribute to it. We first tested it by removing nodes by decreasing degree, showing that root fungal communities in plants grown on agricultural soil were less robust than field margins or the uncultivated field, with the network connectivity sharply decreasing when removing <25% of most important nodes (Fig. 4D). We also found that the number of nodes with high degree (top 25%) was increasing from agricultural soil ($n = 17$), field margin ($n = 27$), and uncultivated field ($n = 36$) and, interestingly, in the agricultural soil none of those ASVs was identified to the genus level while, for other two groups, several nodes were identified as mycorrhizal fungi (e.g., *Acaulospora*, *Funneliformis*, *Glomus*, *Paraglomus*, Fig. 4D). Inferring the Molloy-Reed criterion, we found that all three networks had a giant component ($k > 2$), and we observed higher values of k for plants grown on

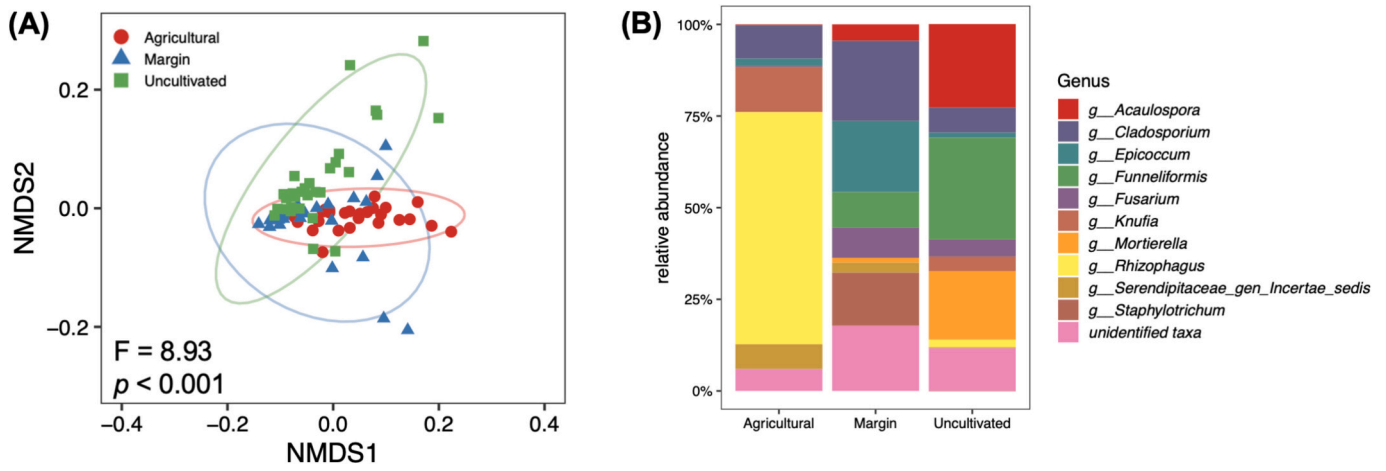


Fig. 1. (A) Non-metric multidimensional scaling (NMDS, stress 0.14) of the root fungal community built on a weighted UniFrac distance matrix, with points colored by soil inoculum. (B) Composition of reads of major fungal genera (relative abundance >1%; relative abundance average across samples) across soil inocula.

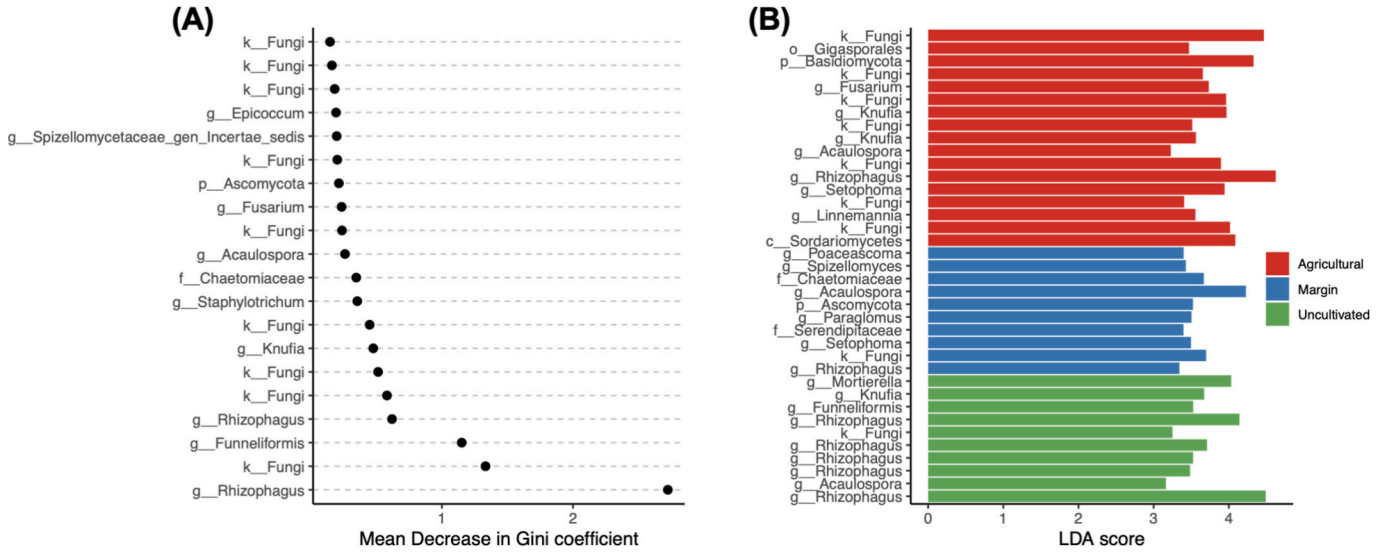


Fig. 2. (A) Random forest analysis of the root mycobiome. The y-axis ranks the top 20 ASVs (identified at the highest confidence taxonomic level) ranked by their importance (Mean Decrease in Gini coefficient) for the group classification. (B) LEfSe bar chart showing the ASVs (identified at the highest confidence taxonomic level) with the strongest association to each of the three soil inocula, and the lengths of the bars (LDA score) indicate the influence of that ASV in discriminating between soils.

agricultural, followed by field margin soil, and uncultivated field soil (Fig. 4E; $F = 3695.6$, $p < 0.001$; all pairwise $p < 0.001$). It is important to note that higher k values can be associated also to higher vulnerability to node removal, as shown in the analysis above (Fig. 4D).

The results above suggest that in our experiment the root fungal microbiome was assembled mainly following stochastic processes, however the network analysis suggested that some taxa might instead be key to network robustness and might not follow the same rules. We thus fit the data from each soil group to a Sloan null model (Sloan et al., 2006), which differentiated taxa following a null-model assembly from those that did not assemble according to a predicted random assembly (Fig. 5A-C). Then, we compared those taxa falling outside the predicted assembly and found that ~14% were shared among the three soils (Fig. 5B), while the widest portion was unique to each soil inoculum. Interestingly, within the shared portion, no ASV was identified beyond the phylum level, while several ASVs unique to each group were identified as mycorrhizal fungi.

4. Discussion

In this study, we found that soil disturbance influences the assembly processes and robustness of the root fungal microbiome. Each soil inoculum produced a distinct root fungal community structure. In addition, we found that the robustness of the root fungal microbiome network (measured as variation in connectivity) decreased along the disturbance gradient, with the most complex and robust networks observed in plants grown on soil from the uncultivated field. Furthermore, our results suggest that stochastic processes, such as dispersal and ecological drift, played a dominant role in shaping fungal community assembly across all soil treatments, although key taxa involved in network robustness, mainly arbuscular mycorrhizal fungi (AMF), did not follow a null-model assembly process.

Our results show that the source of soil inoculum had a strong influence on the structure of root fungal communities. Several studies reported that the origin of soil inoculum is a major driver in structuring plant-associated bacterial (Malacrinò and Bennett, 2024; Malacrinò et al., 2021; Beschoren da Costa et al., 2022; Tkacz et al., 2020;

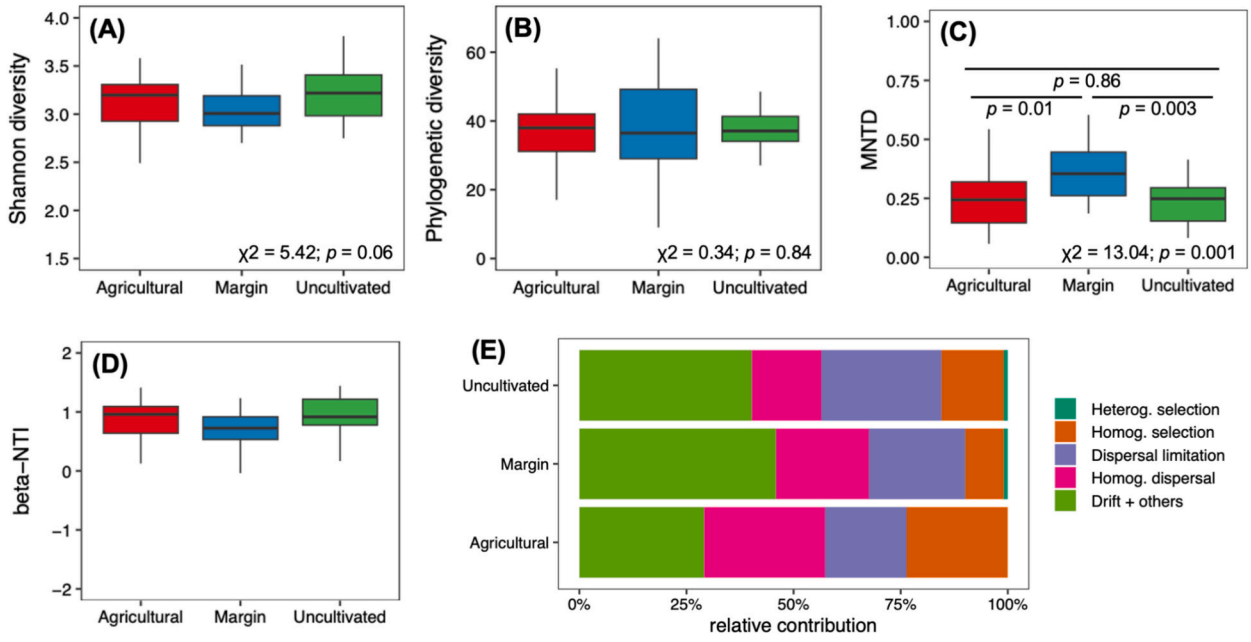


Fig. 3. Comparison of Shannon's diversity index (A), Faith's phylogenetic diversity index (B), and Mean Nearest Taxon Distance (MNTD) metric (C) of the fungal community in roots grown on the three different soils. For all three metrics, we show the results from a linear-mixed effects model and for the MNTD we show the FDR-corrected post-hoc contrasts. (D) β-NTI metric shows values between 2 and -2 suggesting an assembly similar to a null-model. (E) Null- model analysis showing the relative contribution of different processes in the assembly of root fungal communities in the three soils.

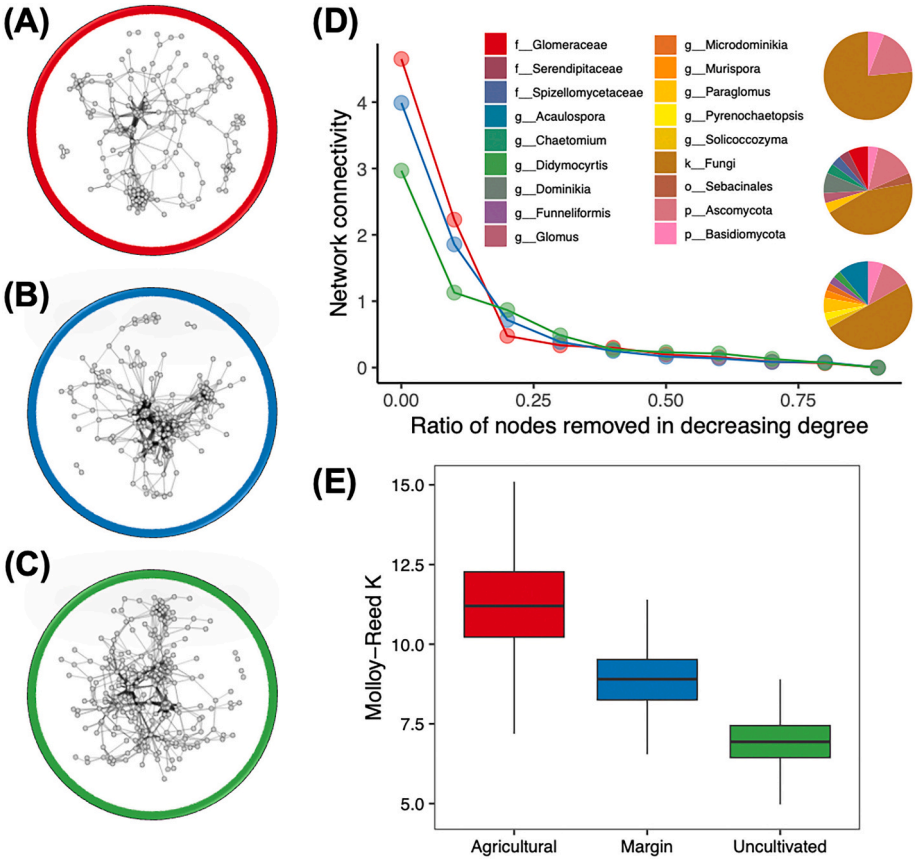


Fig. 4. Fungal co-occurrence network based on correlation analysis for (A) agricultural field, (B) field margin, and (C) uncultivated field. Network robustness was measured as reduction in connectivity in response to removing nodes in decreasing degree (D), and using the Molloy-Reed criterion (E). Inset of panel D shows the taxonomic classification of the top 25% nodes for each soil group: agricultural field (top), field margin (middle), and uncultivated field (bottom).

Zarraonaindia et al., 2015; Hannula et al., 2019) and fungal communities (Beschoren da Costa et al., 2022; Hannula et al., 2021;

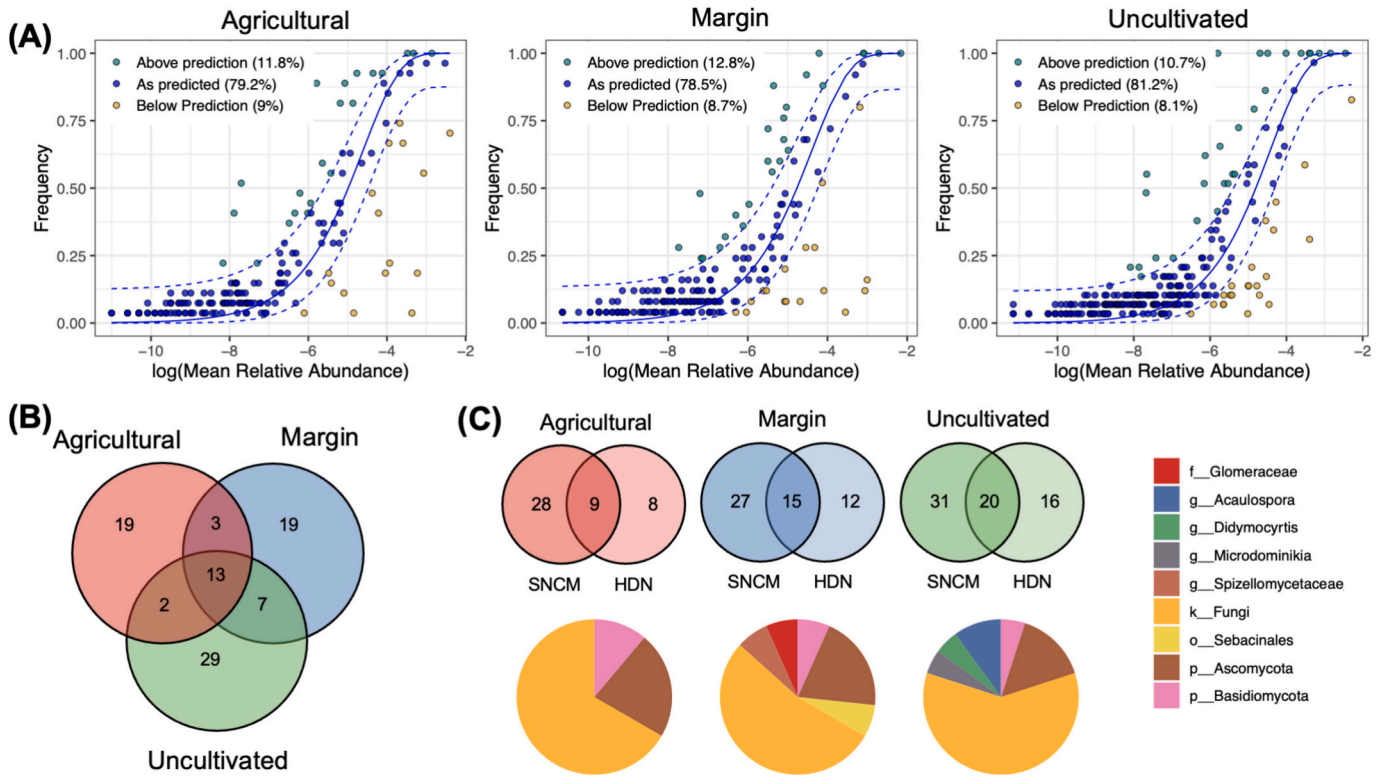


Fig. 5. (A) Fit of root fungal microbial community ASVs to the Sloan null model for plants grown on microcosms inoculated with soil from the agricultural field (left), field margin (center), and uncultivated field (right). (B) Overlap of ASVs not fitting the Sloan null model between the three inocula. (C) Overlap of ASVs not fitting the Sloan null model (SNCM) with the high-degree nodes (HDN), for each soil type, and taxonomic classification (pie charts) for the overlapping ASVs.

Bonito et al., 2019; Almario et al., 2017). Soil origin, similarly to geographic location, might simply determine the initial pool of microorganisms available for root colonization, from which the plant can assemble their own microbiome. While we would have expected differences in fungal diversity between plants grown on soils with different levels of disturbance, we did not observe major changes. Previous studies reported that not all the soil disturbance events influence fungal communities (Beschoren da Costa et al., 2022; Vahter et al., 2022; Rodriguez-Ramos et al., 2021), and no differences in fungal diversity were observed in root fungal communities across samples from farms with different levels of agricultural intensity (Banerjee et al., 2019). However, when looking at the MNTD index, we observed a higher diversity in soil from field margin compared to the other two groups. While it is tempting to link this observation to the intermediate disturbance hypothesis (Santillan et al., 2019), which posits an increase in biological diversity at intermediate levels of disturbance, this result might be simply due to the site-specific microbiome dynamics and further investigations are needed to confirm this result. However, if true, this result would confirm field margins as gatekeeper of biodiversity, as observed in other biological communities (Plath et al., 2021; Crowther et al., 2023; Pérez-Méndez et al., 2025), supporting their importance in safeguarding also the microbial biodiversity in agricultural systems.

Interestingly, we also observed that the root fungal microbiome in our system assembles, mostly, by following stochastic processes. This might be due to the fact that plants were exposed to the inocula for only 6 weeks and fungal communities respond differently from prokaryotic communities (Liu et al., 2024; Romdhane et al., 2022), so that their response to selective forces might need more time to be actually observed, as we noted in our previous short-term study (Mohamed et al., 2024). However, as discussed below, some taxa did not follow stochastic assembly processes.

Environmental disturbance has been previously linked to variation in soil microbiome network properties (Ortiz-Álvarez et al., 2021; Hernandez et al., 2021). In this study, we report for the first time the major role of AMF in the assembly processes and network robustness of the plant root microbiome, bridging and expanding the results from two previous studies. In 't Zandt et al. (2023) used a long-term mesocosm experiment established using soil with minimal disturbance (natural grassland and soil uncultivated for 60 years) to study the relationship between plant community stability and soil microbial networks. While they focused on soil rather than roots, the study observed a reduction in network stability in soil that experienced agriculture, but the authors did not link the effects they observed to any specific taxonomic or functional group. Banerjee et al. (2019), instead, focused on the root fungal microbiome of samples collected in farms performing agriculture at different intensities (conventional, no-till, and organic farming). Similarly to our study, they observed that less intense agriculture has the most robust fungal network, and that AMF are keystone species within these networks. In our experiment, we consider a wider range of disturbance compared to the individual previous studies, and we also show two interesting novel aspects. First, we assessed network robustness by measuring network connectivity after removing nodes/edges randomly or by their order of importance within the network. This allowed us to observe that networks from more disturbed systems are less robust, especially to the removal of high-degree nodes, which were mostly identified as AMF. Second, by null-model analysis, we observed that ~25% of those high-degree nodes are also taxa that, differently from the rest of the microbiome, do not follow stochastic assembly processes. Taken together, these results provide strong evidence of the role of AMF in structuring the root-associated fungal communities and in supporting the robustness of such microbial networks. This is in agreement with the recognized role of AMF in plant ecology and evolution, ecosystem engineers, and gatekeepers of soil health (Zhang et al., 2024; Carrara et al., 2023). Indeed, plant-AMF symbiosis has important consequences for the host, including resistance to stressors, productivity, and overall interactions with other members of the surrounding

biological community above- and below-ground (Shi et al., 2023; Dey and Ghosh, 2022; Vandenkoornhuyse et al., 2015; Müller, 2021; Moora et al., 2025; Sharifi and Ryu, 2021).

Interestingly, in addition to AMF, several ASVs that played a key role in network robustness, and did not follow null assembly processes, were not identified beyond the phylum level. Also, this was more common in soil from the agricultural field and its margins compared to the uncultivated field. Often reference databases used for the taxonomic identification of ASVs, UNITE in our case (Abarenkov et al., 2024), do not include the full available knowledge on environmental fungal isolates because publicly available sequences – the main source for such databases – are often poorly annotated (Abarenkov et al., 2022), reducing our ability to correctly identify the full fungal diversity in a given sample using metagenomics tools. While this might partially explain our observations, we also have to acknowledge that much of the soil biodiversity is still uncovered and many of these microbial taxa might have never been cultured, be unculturable, or difficult to cultivate in vitro (Lewis et al., 2021). However, this less known portion of the soil and plant microbiomes, often called Microbial Dark Matter, might have key functional roles with important consequences for plants (Jiao et al., 2021). This provides support to the shift towards the use of more in-depth techniques, such as shotgun metagenomics and metatranscriptomics (Li et al., 2023), which is much needed and it might revolutionize how we understand plant-microbiome interactions in the wider framework of holobiont biology (Bordenstein et al., 2024; Francomano et al., 2026).

Although we controlled for possible differences in soil chemistry and structure, a wider set of drivers, including the site-specific abiotic environment and vegetation, might have exerted strong selection forces on the soil microbiome and, in turn, on the recruitment of fungal associates in our microcosms. While the controlled microcosm approach allows us to isolate microbial effects from abiotic variation, broader generalization of these patterns across agricultural landscapes will require replicated sampling across multiple sites and management regimes. In addition, while our study provides similar results using different approaches (network analysis, machine learning, and null-model analysis), further experimental evidence is needed to disentangle the role of AMF and other fungal taxa in the assembly of the root microbiome beyond the fungal community, additionally focusing on prokaryotes, nematodes, and other component of the soil- and plant-associated microbial communities. The ITS1–ITS2 primer pair used here provides broad coverage of fungal communities but is known to underrepresent AMF relative to other markers. As a result, the diversity and abundance of AMF are likely underestimated in our dataset. Despite this bias, AMF still resulted to be key contributors to the assembly of root fungal communities, suggesting that their importance in structuring root fungal networks may be even stronger than detected. Future studies using AMF-specific primers or shotgun metagenomics will be needed to fully resolve their contribution to microbiome assembly and stability. Future research should also investigate the functional roles of less known key fungal taxa and explore how these interactions influence plant health under different environmental conditions, further contributing to developing sustainable agricultural practices that harness microbial diversity to improve ecosystem stability and agricultural sustainability.

Overall, our findings provide strong support for the idea that soil disturbance disrupts fungal microbiome assembly and weakens microbiome network robustness in plant roots. By demonstrating that beneficial fungi play a central role in stabilizing root microbiomes, our study supports the importance of maintaining soil biodiversity to promote plant health and ecosystem resilience. This is particularly important considering that plant-microbe interactions in roots and rhizosphere play an essential role in the plant holobiont health and productivity (Vandenkoornhuyse et al., 2015; Bai et al., 2022; Beattie et al., 2024; Sánchez-Cañizares et al., 2017; Berg et al., 2024). Strategies that promote beneficial fungal communities may help mitigate the negative effects of soil disturbance and enhance microbiome resilience. Research in this direction is essential to fully dissect plant-microbiome interactions and deploy microbiome-based strategies to restore and maintain soil and planetary one health (Banerjee and van der Heijden, 2023; Montgomery et al., 2024; Yiallouris et al., 2024; Compant et al., 2025; Singh et al., 2023). Our findings further highlight the critical role of AMF in maintaining stable root microbiomes and suggest that promoting mycorrhizal diversity may be a key strategy for enhancing the resilience of plant communities in the face of increasing environmental disturbance. This is especially important as the resilience of plant communities to the global changes we are facing, and are going to face, much depends on how such changes will impact plant-microbiome interactions (Trivedi et al., 2022; Francomano et al., 2026; Addison et al., 2024), in particular considering that AMF might be more sensitive to global warming than expected (Xu et al., 2022).

CRediT authorship contribution statement

Saveria Mosca: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Edda Francomano:** Writing – review & editing, Investigation. **Meriem Miyassa Aci:** Writing – review & editing, Investigation. **Nesma Zakaria Mohamed:** Writing – review & editing, Investigation. **Leonardo Schena:** Writing – review & editing, Methodology, Funding acquisition. **Antonino Malacrinò:** Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

All authors declare no financial or non-financial competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107187.

Data availability

Data is available on NCBI SRA under BioProject PRJNA1256102. All code to replicate data analysis is available at: https://github.com/amalacrino/mosca_et_al_RootFungalNetwork/.

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