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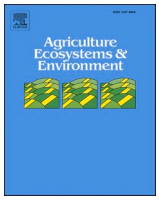

Enrichment in biodiversity and maturation of the soil food web under conservation agriculture is associated with suppression of rice-parasitic nematodes

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ABSTRACT

Meloidogyne spp. and *Hirschmanniella* spp. are among the most damaging plant-parasitic nematodes (PPNs). They threaten rice production, the main staple food in Asia. Cropping systems that promote natural biocontrol and plant tolerance to diseases are put forward as sustainable solutions to protect rice from these pests. In particular, cropping systems managed under conservation agriculture (CA) are promising because they improve soil health and functioning. We investigated the effects of two cropping system components in a Cambodian field, (i) CA practices, i.e., no-tillage with a cover crop *Stylosanthes guianensis* (cv. *Nina*), versus conventional plow-based tillage with no cover crop, and (ii) using IR504, IR64, Azucena and Zhonghua 11 rice varieties, on PPNs in roots and on communities (bacteria, fungi and nematodes) in the rhizosphere. We used a sequencing approach via amplicon barcoding to target microbial marker genes (*16 S* and *ITS rRNA* gene) and a microscopic approach to identify and quantify nematodes in the rhizosphere compartment. The variety had less effect than agricultural practices on the infection by PPNs and on the assembly of the three rhizosphere communities. Under CA, the abundance of PPNs extracted from the roots was reduced by 88%. Soil quality was substantially improved (+83% of total Kjeldahl nitrogen, +34% of available phosphorus, +10% of exchangeable potassium, +110% of soil organic carbon, +30% for the cation exchange capacity), thus providing more basal resources for microbial decomposers, especially fungi (+164% putative saprotrophs). Characterization of the three rhizosphere communities revealed a shift in the structure associated with soil enrichment. Both microbial richness (+3% for bacteria and +38% for fungi) and diversity (Shannon index, +11% for fungi and +5% for nematodes) increased. The relative abundance of taxa was modified by CA with notably more mycorrhizal fungi (+329% *Glomeromycota* spp.) and fewer *Pratylenchidae* nematodes (−92% *Hirschmanniella* spp.) in the rhizosphere. The reassembly of the communities using CA was associated with regulation of PPN populations. The reduction in *Meloidogyne* spp. abundance in roots (−64%) was correlated with the maturity of the food web (maturity index, +10% under CA) and with the increase in the relative abundance of omnivorous nematodes in the rhizosphere (+68% under CA). Seven years of CA in this field enabled the whole soil food web to mature thus creating a favorable niche for potentially predatory nematodes and microbes antagonistic against PPNs. This study confirms that CA is an alternative to nematicides to limit infection by PPNs in rice cropping systems.

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1. Introduction

Rice is the world's main staple crop and is mainly produced in South-East Asia. In Cambodia, it accounts for more than 80% of cultivated land and is the largest export commodity (Yu and Fan, 2011; FAOSTAT, 2018). From 2017–2019, Cambodia was one of the world's top 10 rice-exporting countries, with an annual income of 360 million US$ (FAO, 2020a). Plant-parasitic nematodes (PPNs) are a serious threat to rice production and can reduce yields by 16–80% (Netscher and Erlan, 1993; Soriano et al., 2000), i.e., cause an estimated yield loss of 80 billion US$ per year (Nicol et al., 2011; Jones et al., 2013). *Meloidogyne* (Göeldi, 1892) and *Hirschmanniella* (Sher, 1968) are the two main genera of PPNs that affect rice production in South-East Asia (De Waele and Elsen, 2007; Mantelin et al., 2017). *Meloidogyne*, also known as root-knot nematodes, are sedentary endoparasitic nematodes and cause the formation of galls on the roots, whereas *Hirschmanniella* are migratory endoparasitic nematodes. These parasites damage the root architecture, disrupt water and nutrient transport through the roots and increase crop susceptibility to other diseases (Kyndt et al., 2017).

Methods to reduce PPN infection are available, but all have limitations. For example, although next-generation nematicides are now available on the market, they still have an environmental cost and are toxic to non-target organisms (Ebone et al., 2019; Oka, 2020). Another method of control is using rice genotypes that are resistant to PPNs. Some resistance genes have been identified, but they are rare and occur mainly in sparsely cultivated rice species (e.g., *Oryza glaberrima*), making it difficult to transfer useful traits to widely grown rice varieties. A few rare resistant *Oryza sativa* varieties have been identified, but their introgression may have yield penalties or confer undesirable agronomic traits (Fuller et al., 2008; Mantelin et al., 2017). In addition, an increasing number of resistance-breaking nematode pathotypes is being reported, thus requiring continuous efforts by rice breeders to select varieties that are resistant to new nematode pathotypes (Davies and Elling, 2015; Phan et al., 2018). Finally, traditional cultivation systems mainly based on water management (continuous flooding) had been used for centuries to control rice PPNs and reduce yield losses, but tillage followed by seed broadcasting on non-flooded rice fields has become the most common cultivation system in recent decades, notably due to the Green Revolution (Pingali, 2012) and the increasing scarcity of water and labor (Thrall et al., 2010).

New agricultural approaches have emerged a few decades ago, that aim at replacing external inputs by improved management of ecological processes (Altieri, 1989). In these systems, farmers seek to optimize biotic and abiotic interactions within agroecosystems to limit the prevalence of pests and diseases. These "ecologized agricultures" (*sensu* Ollivier and Bellon, 2013) emphasize the importance of soil biodiversity and rely on agroecosystem self-regulation. Soil organisms indeed provide a wide range of ecosystem services, including pest and disease regulation (Kibblewhite et al., 2008). Nematodes (also called nematofauna) are excellent indicators of soil functions (Bongers and Ferris, 1999; Yeates, 2003; Villenave et al., 2009a). The abundance and diversity of nematodes provides insights into the soil biological functioning as they occupy different levels of the soil food web (Ekschmitt et al., 2001). While some nematodes are parasitic (i.e., PPNs and entomopathogenic nematodes), others regulate bacterial and fungal populations (bacterivorous and fungivorous nematodes) or feed on other organisms including nematodes (predatory nematodes). Studying the structure and assembly of these communities provides insights into the effects of biological activities in soil on plant health.

Plants and their associated microbes, grouped under the term "microbiota" (Berg et al., 2020), form an assemblage of co-evolved species, also termed "holobiont" (Hassani et al., 2018). The assembly of the rice-associated microbiota has been shown to be driven by a variety of factors (Edwards et al., 2015) including the host genotype (Hardoim et al., 2011; Tabrett and Horton, 2020) and cultivation practices. Many studies have shown that plants can modulate their associated above- or below-ground microbiota to dynamically adjust to their environment (Vandenkoornhuyse et al., 2015) via signaling (Venturi and Keel, 2016) and root exudation (Vives-Peris et al., 2020). Plants can recruit beneficial microbes to defend against soil-borne pathogens (Liu et al., 2021; Berendsen et al., 2012). Phytobeneficial microbes can prevent plant diseases either by promoting plant growth and development (Bhattacharyya and Jha, 2012; Vejan et al., 2016) or through antagonistic effects on pathogens (Mhatre et al., 2019; Stirling, 2014). Suppressive soils are a natural source of microbiota with a high potential to suppress PPNs, including root-knot nematodes (Topalovic et al., 2020) and cyst nematodes (Hussain et al., 2018). However, soil suppressiveness is induced by both biotic (Mazzola, 2002; Schlatter et al., 2017) and abiotic factors (Agler et al., 2016; Islam et al., 2020). In rice cropping systems, there is an insufficient understanding of the effects of different agricultural practices and varieties on the assembly of rhizosphere communities, in particular bacteria, fungi and nematodes.

Conservation agriculture (CA) can be considered as an "ecologized" cropping system that improves soil health and functioning (FAO, 2020b). It relies on minimum soil disturbance (reduced or no-tillage), permanent soil cover (living cover crops or dead organic matter) and crop rotations (as long and diversified as possible). These practices have significant impacts on soil communities. A previous study showed that the use of no-tillage and cover crops has improved soil physicochemical properties (SOC and nutrient availability) and increased microbial biomass (bacteria and fungi) during the three-year rotation of rice, corn and soybean in Laos (Lienhard et al., 2013). Microbial functional diversity was also increased under CA (Tang et al., 2020), suggesting that CA practices can improve crop tolerance to pathogens (van Elsas et al., 2002; Doni et al., 2019; Wang et al., 2020). For instance, a study showed that the use of no-tillage and crop rotation helped control the rice cyst nematode *Heterodera elachista* (Ito et al., 2015a). However, the potential of CA in PPN control in rice under irrigated conditions and it effects on the microbiota and the nematofauna at the plant-soil interface have not yet been fully understood.

To assess the potential of CA to improve plant health, an experiment was set up in 2011 in a lowland and sandy rice field in Stung Chinit, Kampong Thom province, Cambodia. The field was managed under either conventional plow-based tillage (hereafter CT), or a type of CA with direct sowing of rice on cover crops crushed with a roller to form a layer of mulch before sowing, and with no tillage. In 2018, seven years after the transition to CA, we observed a reduction in the abundance of PPNs in roots under CA compared to CT, and investigated which soil parameters were linked with this reduction. In this study, we hypothesized that the reduction in the abundance of PPNs was associated with modifications in the soil food web caused by the cropping system. Thus, we characterized the communities of bacteria, fungi and nematodes in the rice rhizosphere in response to two components of the cropping system, agricultural practices and the rice variety. More specifically, parasitism, soil properties and community assembly of the three rhizosphere communities were investigated in four varieties (two *O. sativa indica* named IR504 and IR64, and two *O. sativa japonica* named Azucena and Zhonghua 11, the latter being resistant to *Meloidogyne graminicola*) grown using CA and CT. We analyzed the α- (richness and Shannon index) and β- (structure and dispersion) diversity, the relative abundance of taxa and guilds and their specific enrichments in each community. Finally, we discussed correlations observed between the reduction in PPN abundance and soil parameters, biodiversity or soil food web indices.

2. Material and methods

2.1. Field characterization, past management practices and experimental design

The field experiment was established in April 2011 on a 2.6 ha tropical lowland rice parcel in Stung Chinit, Santuk district, Kampong

Thom province, Cambodia (12°32′55″N; 105°08′47″E) (Fig. S1). Most rainfall in this region occurs in the early wet season (April to July) and the main wet season (July to October). The soil is a sandy loam (~ 69% sand, 18% silt and 13% clay) belonging to the "Prey Khmer group" in the Cambodian agronomic soil classification system (White et al., 1997), equivalent to red-yellow podzols according to the FAO soil taxonomy (Suong et al., 2019). To explore shifts in soil microbial ecology caused by the two practices and different rice genotypes, a field plot experiment compared conventional tillage, (CT) and a no-till mulch-based cropping system, a component of conservation agriculture, (CA) using four different *O. sativa* varieties. Because the agricultural practice was a hard to change factor, and since the field was large enough to be divided, a split plot design was used (Altman and Krzywinski, 2015). The field was divided into eight whole plots (four for CT, four for CA), each of which was split into four subplots (Fig. S1). Each of the eight whole plots had an area of 55 m2 (13.75 × 4 m). Agronomic practices were assigned to whole plots following the long-term (seven years of CA/CT practice) of the land. Within a whole plot, rice varieties were distributed across subplots using a randomized complete block design (RCBD). Agricultural practices were the factor for the whole plot and rice varieties were the factor for the subplots.

Before the experiment, in 2017, two rice cycles of *O. sativa indica* were cultivated: IR504 sown as an early wet season rice in March and Phka Rumduol sown in July. After harvesting in 2017, under CT, the soil remained bare until it was plowed and rice was sown for the 2018 season. Under CA, before the harvest of the second rice cycle (Phka Rumdoul) in mid-November 2017, seeds of *Stylosanthes guianensis* (cv. Nina), a legume cover crop, were broadcast (8 kg/ha). On March 15, 2018, two weeks before rice was sown, the cover crop was terminated by rolling twice with a roller-crimper followed by the application of a mix of 3 l/ha of glyphosate (N-(phosphonomethyl)glycine) and 1 l/ha of 2,4-D (2,4-dichlorophenoxyacetic acid) immediately after rolling.

On March 28, 2018, four rice varieties were sown per block: two varieties of *O. sativa indica* (IR504 and IR64) and two varieties of *O. sativa japonica* (Azucena and Zhonghua 11). These varieties are not photosensitive and have a relatively short cycle (less than four months). We chose the different varieties based on their use in Cambodia and their different responses to PPN infection. The IR64 variety was developed by IRRI in 1985 with a combination of many valuable traits including high yield, quality and disease resistance (Mackill and Khush, 2018), although it is sensitive to PPNs such as *M. graminicola* (Phan et al., 2018). Azucena is the most sensitive to PPNs (data not shown); Zhonghua 11 was the only resistant variety in our set (Phan et al., 2018). Prior to sowing, a base dressing with 200 kg/ha of thermophosphate (16% P_2O_5, 28% CaO, 18% MgO) was applied. The varieties were sown by hand by inserting four to five seeds into three-centimeter deep holes at ten-centimeter intervals in a straight row. Three four-meter long rows of each variety spaced 30 cm apart were planted in each block. In all rows, 120 holes were filled with a total of 3840 to 4800 seeds. Following sowing, a top dressing was applied with 100 kg/ha of DAP (diammonium phosphate, 16 N-20P2O5–0K2O/ha), 50 kg/ha of KCl (potassium chloride, 30 kg K2O/ha) and, after 30 days, 75 kg/ha of urea (34.5 kg N/ha) on the whole field (CA and CT plots). One day after sowing, it was treated with 1 l/ha of 2,4-D and 0.15 l/ha of organic vegetable oil to control weed development.

2.2. Plant and soil sampling

Sampling was done one month after sowing (May 1, 2018) when the lowland field was not under water. Sampling was done in the block corresponding to each variety and each type of agricultural practice, giving a total of 32 samples. Ten plants per condition were carefully extracted for each analysis to identify the nematofauna in the rhizosphere and the abundance of PPNs in the roots. Intact soil cores (30 cm deep, 20 cm diameter) containing the rice root system of five plants per condition were also sampled. The five plants per condition were extracted from these soil cores to characterize the microbial communities (bacteria and fungi) and the soil surrounding the rice roots were collected and pooled to create a composite sample per condition for soil analysis. All the samples for analysis of the rhizosphere compartment were taken in the middle rows in order to avoid edge effects. Samples were immediately placed in plastic bags, transported to the laboratory and stored at 4 °C until analysis.

2.3. Soil analysis

Soil properties were analyzed using the methods described in detail in Motsara and Roy (2008). Briefly, soil samples were air-dried at room temperature and pH was determined using a 1:2:5 ratio of soil:distilled water:KCl 1 M mixture and measured with a pH meter D-51 (Horiba Ltd., Kyoto, Japan). Available phosphorus (P) was determined with the Bray II method, exchangeable potassium (K) with a flame photometer, soil organic carbon (SOC) using the Walkley and Black method, total Kjeldahl nitrogen (TKN) using the method of Kjeldahl, and cation exchange capacity (CEC) using the ammonium acetate method.

2.4. PPN abundance in roots

Plant-parasitic nematodes (PPNs) were extracted from fresh root samples following the method of Bellafiore et al. (2015). Briefly, the samples were placed in a 0.6% hypochlorite solution for three minutes and ground in a blender to extract nematode eggs and juveniles. The mixture was then filtered through a series of 250, 75 and 25 μm sieves before being collected on the 25 μm one. Juveniles belonging to the genera *Meloidogyne* spp. and *Hirschmanniella* spp. were counted under the microscope, in addition to all the PPN eggs, and were reported as abundance of PPNs/g of root.

2.5. Nematofauna processing

The nematofauna in the soil surrounding the roots (the rhizosphere) of the fresh plant samples was analyzed by ELISOL Environnement (Congénies, France) using the standard ISO 23611-4 (2007) procedure. The nematodes in each sample were extracted from 150 g of composite fresh soil sample using a modified elutriation system (Seinhorst, 1962; Villenave et al., 2009b). After fixing in a formalin glycerol mixture and transferring to slides, the composition of soil nematofauna was determined at family level (and genus level if possible) through microscopic observation at 400x magnification. A total of 44,019 nematodes were counted (min = 202, median = 1369, max = 2789). Nematode density was recorded as the total number of individuals/100 g of dry soil. Food web indices as defined by Ferris and Bongers (2006, 2009) in the rhizosphere were also calculated: EI: enrichment index (a measure of resource availability, especially nitrogen, and activity of primary decomposers); SI: structural index (a measure of the degree of trophic links, stability and capacity to recover from stress calculated with the slow-growing and reproducing predatory and omnivorous nematodes with c-p values of 3, 4 and 5); IVD: index of organic matter decomposition (a measure of primary organic matter decomposition, also known as nematode channel ratio of the fungal-feeders over the bacterial-feeders), and MI: maturity index (a measure of environmental disturbance and stability based on free-living nematodes).

2.6. Microbiome processing

Bacterial and fungal communities in the rhizosphere of the fresh plant samples were analyzed using molecular techniques. DNA was extracted from a 0.25-g composite sample of the rhizosphere using the PowerSoil® DNA Isolation Kit (Qiagen, Netherlands) following the manufacturer's instructions. Samples were pooled and each contributed exactly the same amount (50 ng/μl) of DNA in the final library. PCR amplification, library and MiSeq Illumina sequencing were performed

by Macrogen (Seoul, South Korea) using bacterial primers 341 F (16S_V3F, 5'-CCTACGGGNGGCWGCAG-3') and 805 R (16S_V4R, 5'-GACTACHVGGGTATCTAATCC-3') to amplify the V3-V4 region of the 16S rDNA gene (Sinclair et al., 2015), and fungal primers ITS3F (5'-GCATCGATGAAGAACGCAGC-3) and ITS4R (5'-TCCTCCGCTTATTGATATGC-3) to amplify the rDNA-ITSII region (White et al., 1990; Mitchell and Zuccaro, 2006). The sequencing data for this study are accessible in the ENA database under the accession number PRJEB47939.

The data were analyzed using the QIIME 2 (v2020.2) pipeline (Bolyen et al., 2019) on the IRD i-Trop cluster. The function *DADA2 denoise-paired* (Callahan et al., 2016) with default parameters was used to correct sequencing errors, to infer exact amplicon sequence variants (ESVs) and to remove chimeric sequences. For bacteria, forward and reverse reads were trimmed at 17 and 21 bp, respectively, to remove primers and adapters, quality-truncated at 274 and 210 bp respectively, and merged with a minimum overlap of 20 bp. For fungi, only forward reads were processed according to the method of Pauvert et al. (2019) and 20 bp were trimmed to remove primers. Taxonomic affiliations were assigned by a naive Bayes classifier which was trained for the V3-V4 region using the database SILVA 138 for bacteria and the database UNITE 04.02.2020 (all eukaryotes) for fungi.

Approximately 33% and 74% of input reads passed the denoising and chimera filters for the 16 S marker and the ITS marker, respectively. We subsequently filtered out plasts (chloroplasts and mitochondria) and other unwanted ESVs (unassigned at domain level or assigned to *Eukaryota*) to keep only ESVs assigned to the *Bacteria* or *Archaea* kingdoms for the 16 S marker. Removed reads accounted for 0.5% of the total preprocessed reads. Only 42 ESVs were assigned to *Archaea* and were consequently filtered out in the phyloseq object before analysis. For the ITS marker, we filtered out unassigned ESVs at domain level. Removed reads accounted for 25.5% of the total preprocessed reads. Then we kept only ESVs assigned to the *Fungi* kingdom. Removed reads accounted for 36.3% of the total preprocessed reads. Finally, we ended up with 99.5% and 38.2% of the total preprocessed reads for the 16 S marker and the ITS marker, respectively. We used the microscopy-based approach to identify and quantify the nematodes, because of the difficulty involved in obtaining DNA from a community of nematodes, the lack of appropriate primers and of public databases (Geisen et al., 2018; Schenk et al., 2020). According to the rarefaction curves (Fig. S2), the samples reached a plateau, meaning the sequencing depth was sufficient so there was no need to rarefy the datasets (McMurdie and Holmes, 2013). Only one sample of nematofauna (CA, Zhonghua 11, repetition 3) did not reach the plateau and was consequently discarded from the analysis. The scripts for the hereinabove QIIME 2 pipeline and the following R analyzes written for this study are available on GitLab under the project ID 27138799 (soilfoodwebunderCA_stungchinit_2018).

Analyzes were performed using R software, version 4.0.3 (R Core Team, 2020). The packages *dplyr* (Wickham et al., 2021a), *magrittr* (Milton Bache et al., 2020), *tidyverse* (Wickham et al., 2019), *tidymodels* (Kuhn and Wickham, 2021) and *stringr* (Wickham, 2019) were used to handle the data. The packages *phyloseq* (McMurdie and Holmes, 2013), *microbiome* (Lahti et al., 2017), *eulerr* (Larsson, 2020) were used to draw the Venn diagrams, and *vegan* (Oksanen et al., 2020a,b) was used to analyze the community metrics. Non-metric multidimensional scaling representations (NMDSs) based on Bray-Curtis distances were drawn using the function *metaMDS*, the homogeneity of the multivariate dispersions was tested using the function *vegdist*, dispersion was tested using the function *betadisper*, the effects of the treatment on community structure were tested with a permutational multivariate analysis using the functions *permutest* and *adonis* with "practices" (agricultural practices) and "variety" (rice variety) as fixed effect and "block" as random factor, and correlations between the structure of the communities and environmental variables were explored using the function *envfit*.

The packages *nlme* (Pinheiro et al., 2021), *lme4* (Bates et al., 2015), *MASS* (Venables and Ripley, 2002), *car* (Fox et al., 2021), *multcomp* (Hothorn et al., 2008) and *emmeans* (Russel et al., 2021) were used for statistical analyses. A linear mixed model (function *glm*) with "practices" and "variety" as fixed effect and "block" as random factor was fitted. In the case of non-normality, data were transformed by $f(x) = \log10(x + 1)$ for PPN abundance in the roots and $f(x) = \log10(x)$ for the soil variables (function *lme*, package *nlme*). A generalized linear mixed model (function *glmer*, package *lme4*) was used for the analysis of the diversity (family = "poisson" for the richness and family = gaussian(link = "identity") for the Shannon index. The effects "practices" and "variety" (with interaction term) were assessed using analysis of variance (ANOVA) followed by a Tukey's honest significant difference (HSD) post hoc test, and were considered significant at $p < 0.05$. Estimated marginal means (least-squares means) were obtained with the functions *cld* (package *multcomp)* and *emmeans* (adjust = "tukey").

We used the package *DAtest* (Russel et al., 2018) for differential abundance testing of features. Hereafter, the term 'features' refers to bacterial and fungal exact sequence variants (ESVs) obtained by the amplicon barcoding and bioinformatic taxonomic assignments, or to the nematode families counted and identified using the microscopy-based approach. Enrichments were analyzed on each variety and type of practice after trimming low abundant features (min.samples = 3, min. reads = 10). The best statistical tests (LIMMA for the microbiota and negative binomial for the nematofauna) were used. Features were then filtered based on significance ($p < 0.05$). Bacteria, fungi and nematodes were assigned to guilds using respectively the FAPROTAX (Louca et al., 2017), FUNGuild (Nguyen et al., 2016) and NEMAPLEX (Ferris, 1999) databases. Functional guilds were divided into two non-overlapping groups: group 1 included reactions with chemical elements and the use of small molecules (manganese oxidation, methanol oxidation, methanotrophy, nitrate reduction, nitrification and respiration of sulfur compounds) and group 2 included degradation of larger molecules or polymers and fermentation processes (xylanolysis + fermentation, ureolysis + fermentation, ureolysis, hydrocarbon degradation, fermentation + aromatic compound degradation, fermentation, chlorate reducers, chitinolysis, cellulolysis and aromatic compound degradation). Among the 11,919 bacterial ESVs, a total of 788 (6.6%) were assigned, 572 to group 1 and 416 to group 2. For the putative fungal trophic guilds, among the 2062 ESVs, 756 (36.7%) were found in the database (140 highly probable, 346 probable and 270 possible) that could be attributed to one or several of the three trophic modes (symbiotrophy, saprotrophy and pathotrophy). All nematodes were assigned to one of the following trophic groups (Yeates et al., 1993): plant-feeding (including facultative or obligatory plant-feeding nematodes), fungal-feeding, bacterial-feeding, unicellular eukaryote-feeding (including nematodes feeding on protists, fungal spores and whole yeast cells), predatory (including predators of nematodes that are mainly specialist) and omnivorous (including nematodes feeding on a combination of fungi and unicellular eukaryotes, and including predators of nematodes that are mainly generalists). In addition to their trophic group habit, nematode families were assigned to a structural guild that characterize their life strategy (from copiotroph to persistor, Bongers and Bongers, 1998) defined as: cp1 for enrichment opportunists, cp2 for basal fauna, cp3 for early successional opportunists, cp4 for intermediate succession and disturbance sensitivity, and cp5 for long-lived intolerant species.

Finally, the packages *Hmisc* (Harrell, 2021) and *corrplot* (Wei et al., 2021) were used for correlation analysis (type = "spearman", adjust = "fdr"). Drawings were done with the packages *ggplot2* (Wickham, 2009), *cowplot* (Wilke, 2020) and *svglite* (Wickham et al., 2021b). *Inkscape* software was used to finalize the figures.

3. Results

3.1. Reduction in PPN abundance in roots under CA

The abundance of PPNs extracted from the rice roots (Fig. 1 and

Table S1) revealed significant effects of both cropping system components (agricultural practices and the rice variety). The abundance of *Meloidogyne* spp. depended on both the variety (Fig. 1A, $p < 0.001$) and the type of practices (Fig. 1B, $p < 0.001$). We observed a reduction of around 64% in *Meloidogyne* spp. under CA (35 ± 32 PPNs/g of roots) compared to under CT (98 ± 85 PPNs/g of roots) with variability depending on the variety. The fewest *Meloidogyne* spp. were found in the roots of the resistant Zhonghua 11 variety (26 ± 23 PPNs/g of roots) and the most in the roots of the Azucena variety (139 ± 103 PPNs/g of roots). The abundances in IR504 and IR64 roots were intermediate: respectively 45 ± 37 and 55 ± 37 PPNs/g of roots. For *Hirschmanniella* spp., we observed a tendency to a reduction under CA (1 ± 4 PPNs/g of roots) compared to under CT (3 ± 4 PPNs/g of roots), although the reduction was not significant (Fig. 1D, $p = 0.216$). A similar trend was observed for *Meloidogyne* spp. with the variety effect (Fig. 1C), Zhonghua 11 having the lowest abundance of *Hirschmanniella* spp. (0 ± 0 PPNs/g of roots) and Azucena the highest (4 ± 6 PPNs/g of roots). The effects of the cultivation practices ($p < 0.001$, Fig. 1F) and of the rice variety ($p < 0.01$, Fig. 1E) were significant when the total abundance of these two genera of PPNs included the eggs of all PPNs: fewer PPNs were present under CA (65 ± 50 PPNs/g of roots) than under CT (560 ± 518 PPNs/g of roots) and again the Zhonghua 11 variety harbored fewer PPNs than the other varieties (93 ± 95, 331 ± 257, 379 ± 581, 447 ± 606 PPNs/g of roots for Zhonghua 11, Azucena, IR504 and IR64, respectively).

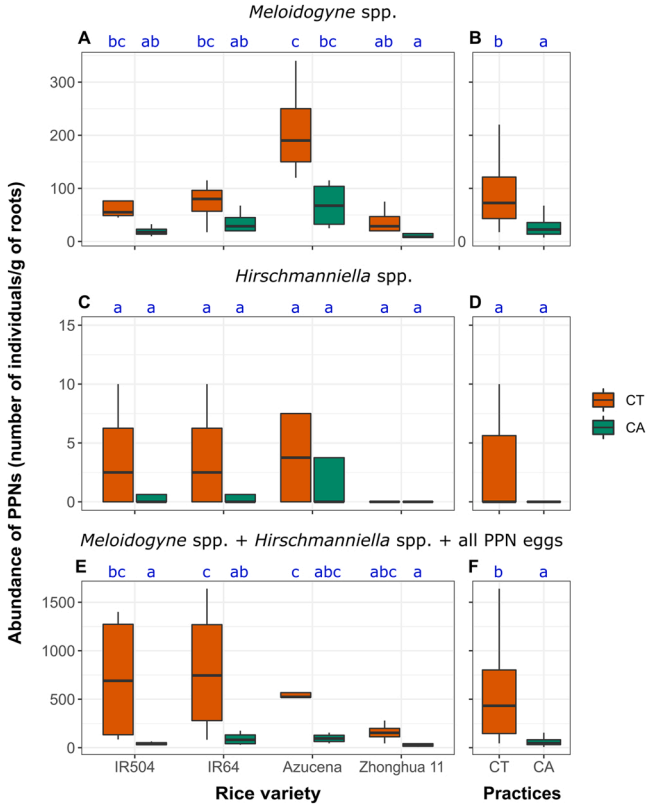

Fig. 1. Abundance of plant-parasitic nematodes (PPNs) in roots of four rice varieties (IR504, IR64, Azucena and Zhonghua 11) managed under conventional tillage (CT) or conservation agriculture (CA). Effects of the rice varieties in the left panel (A, C and E) and effects of the practices (all varieties combined) in the right panel (B, D and F). Abundance of *Meloidogyne* spp. (A and B), *Hirschmanniella* spp. (C and D) or the sum of both genera in addition to all PPN eggs (E and F) were measured by the number of individuals/g of roots and assessed by an estimated marginal means (groups are indicated on top of each bar) using a mixed linear model of the number of individuals +1 with a log scale (including a random effect for the block).

3.2. Enrichment in soil organic matter and nutrients under CA

Agricultural practices impacted six out of the seven soil variables measured: with the exception of pH, all the variables were significantly higher under CA than under CT (Tables 1, S2). There was an increase of 110% in SOC ($p < 0.001$), 83% in TKN ($p < 0.001$), 34% in available P ($p < 0.001$), 30% in CEC ($p < 0.001$) and 10% in exchangeable K ($p < 0.05$).

3.3. Effects of the cropping system on the diversity of the rhizosphere communities

Amplicon sequencing yielded a total of 1,095,186 reads (min = 28,341, median = 33,892, max = 45,755) for the 16 S marker and 1,153,809 reads (min = 25,131, median = 37,635, max = 42,549) for the ITS marker with all samples having more than 1000 read counts. Finally, for the microbiota, we obtained 361,889 high quality reads with a median of 10,832 reads per sample (min = 7510 and max = 17,834) assigned to a total of 11,919 ESVs for bacteria, and 326,487 high quality reads with a median of 10,234 reads per sample (min = 4471 and max = 16,476) assigned to a total of 2062 ESVs for fungi. These microbial ESVs were shared or specific to the cropping system components within the bacterial (Fig. 2A and D) or fungal (Fig. 2B and E) communities. The fraction shared by both types of practices was larger for fungal ESVs (17%) than for bacterial ESVs (12%). The remaining ESVs were specific to either CT or CA. The fraction of fungal ESVs specific to CA was relatively larger (50% under CA compared to 33% under CT) than the fraction of bacterial ESVs (46% under CA compared to 42% under CT). The fraction of fungal ESVs shared by all varieties was larger (13%) than the fraction of bacterial ESVs (8%). The fraction of bacterial ESVs specific to each variety was 19% and the fraction of fungal ESVs was 16%. For nematodes, we obtained 32 families in total. All nematode families found under CT were also found under CA (Fig. 2C). A few more were specific to CA (22%). Most of the nematode families were shared by all four varieties (69%), very few were specific to a particular variety (9% to Azucena, 3% to IR504) and none to Zhonghua 11 or IR64 (Fig. 2F).

The components of the cropping system had an effect on the diversity of both the microbiota (bacteria and fungi) and of the nematofauna (Fig. 3 and Table 2). First, there was a shift in β-diversity induced by practices (Fig. 3A–C) that explained around 25% of the variance in the structure of all three rhizosphere communities (Table 2), bacteria being the least impacted ($R^2 = 0.21$, $p < 0.001$). The dispersion of the nematofauna ($F = 12.67$, $p < 0.01$) was higher under CA than under CT. The variety had no significant effect on β-diversity. Soil properties were correlated with the structure of the three communities (Fig. S3): the increases in SOC, TKN, available P and CEC were correlated with the shift of the structure of the three rhizosphere communities toward CA. In addition, pH was positively correlated with the shift of the fungal

Table 1
Effects of agricultural practices on soil properties.

Soil properties	CT	CA
pH	5.32 ± 0.09	5.23 ± 0.16
avail. P (ppm)	**13.85 ± 3.34**	**18.57 ± 4.02**
exch. K (meq/100 g)	**0.29 ± 0.05**	**0.32 ± 0.04**
TKN (%)	**0.030 ± 0.008**	**0.061 ± 0.011**
SOC (%)	**0.95 ± 0.28**	**1.99 ± 0.27**
CEC (meq/100 g)	**8.78 ± 2.01**	**11.41 ± 2.19**

Effect of practices (CA: conservation agriculture versus CT: conventional tillage) on soil properties as assessed by an anova on a mixed linear model of the soil properties with a log scale (including a random effect for the block). Means ± standard deviations for the pH, available phosphorus (avail. P), exchangeable potassium (exch. K), total Kjeldahl nitrogen (TKN), soil organic carbon (SOC) and cation exchange capacity (CEC). Statistically different soil properties are in bold and F-values for the effect of the practices are in Table S2 with minor effect of the rice varieties (IR504, IR64, Azucena and Zhonghua 11).

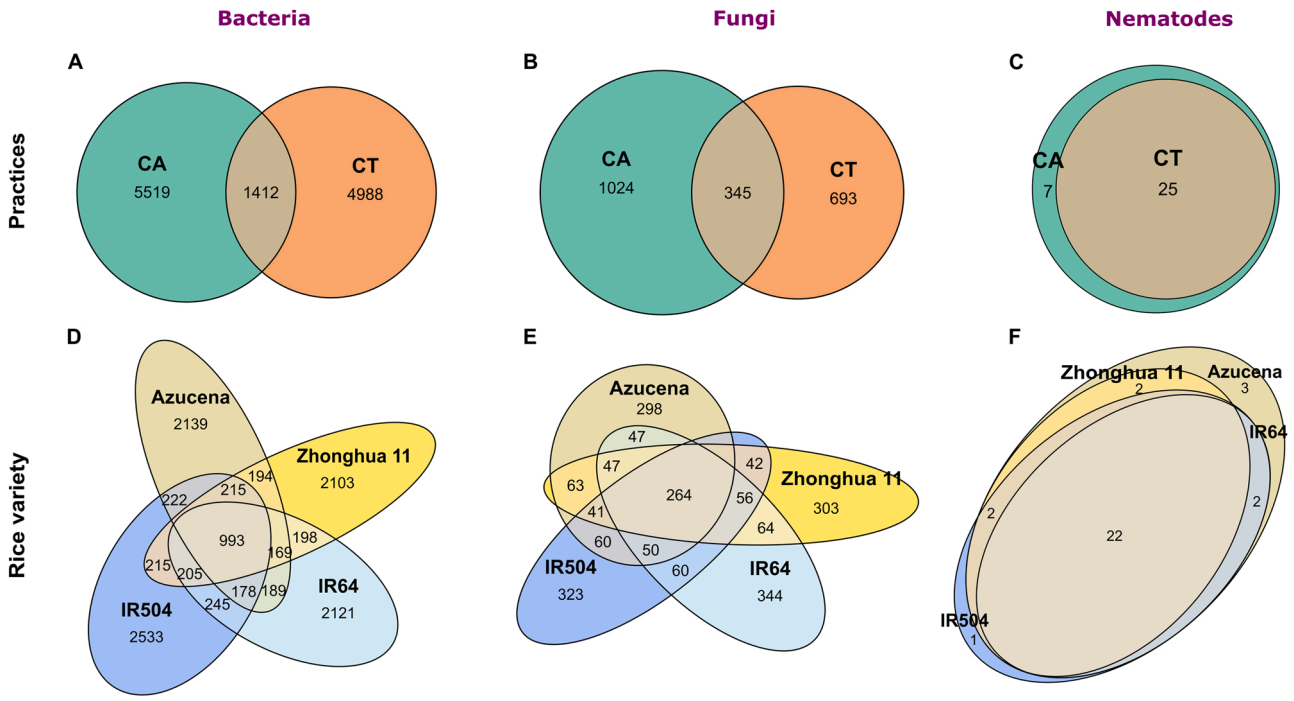

Fig. 2. Venn diagrams of the rhizosphere communities of bacteria (A and D), fungi (B and E) and nematodes (C and F). The numbers indicate the feature counts (ESVs for bacteria and fungi, or microscopically identified families for nematodes) shared between the types of agricultural practices (CT: conventional tillage and CA: conservation agriculture) (A, B and C) and the rice varieties (IR504, IR64, Azucena or Zhonghua 11) (D, E and F).

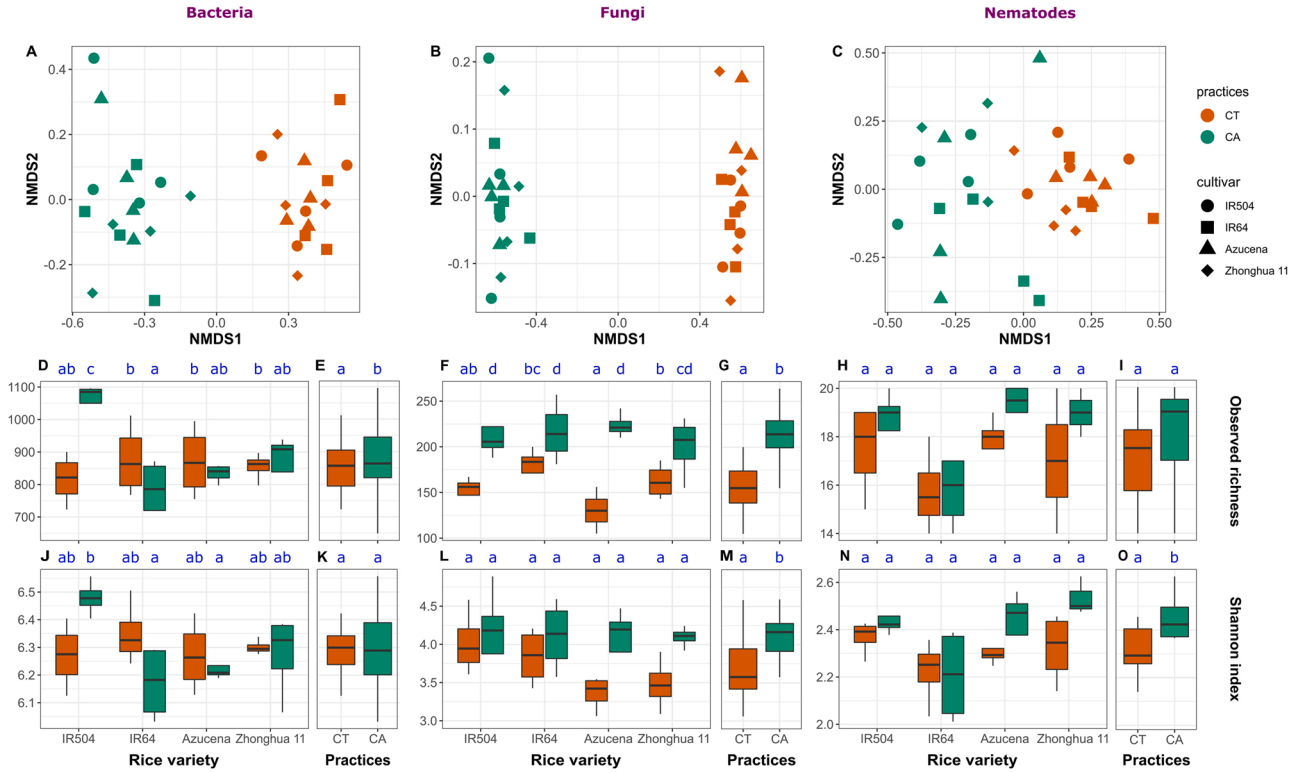

Fig. 3. Diversity of the communities of bacteria (A, D, E, J and K), fungi (B, F, G, L and M) and nematodes (C, H, I, N and O) in the rhizosphere of the four rice varieties (IR504, IR64, Azucena or Zhonghua 11) managed under conventional tillage (CT) or conservation agriculture (CA) as represented by non-metric multi-dimensional scalings (NMDSs) based on Bray-Curtis distances (A, B and C), observed richness (from D to I) and Shannon index (from J to O) assessed used estimated marginal means (groups are indicated at the top of each bar) in a generalized linear mixed model of the diversity index with a Poisson distribution for the observed richness or a Gaussian distribution for the Shannon index (including a random effect for the block). Detailed effects of practices and rice variety on these diversity indices are given in Table 2. Soil variables projected on top of the NMDSs in Fig. S3. Stress plot = 0.10 (A), 0.080 (B) and 0.20 (C).

Table 2
Effects of agricultural practices and rice varieties on the β- and α-diversity of the rhizosphere communities of bacteria, fungi and nematodes.

	Bacteria				Fungi				Nematodes			
	β-diversity		α-diversity		β-diversity		α-diversity		β-diversity		α-diversity	
	Structure	Dispersion	Richness	Shannon	Structure	Dispersion	Richness	Shannon	Structure	Dispersion	Richness	Shannon
	R^2	F	Chisq	chisq	R^2	F	chisq	chisq	R^2	F	chisq	chisq
Practices	**0.21** ***	0.01(NS)	**7.25** **	0.06(NS)	**0.28** ***	2.97(NS)	**146.83** ***	**5.81** *	**0.28** ***	**12.67** **	0.43 (NS)	**7.40** **
Varieties	0.08 (NS)	0.95 (NS)	**64.79** ***	6.96 (NS)	0.09 (NS)	0.73 (NS)	**9.06** *	3.21 (NS)	0.07 (NS)	0.31 (NS)	0.52 (NS)	**13.26** **
Practices × Varieties	0.08 (NS)		**137.50** ***	**13.89** **	0.08 (NS)		**26.70** ***	2.35 (NS)	0.07 (NS)		0.97 (NS)	2.81 (NS)

Effects of the practices (CA: conservation agriculture versus CT: conventional tillage) and the four rice varieties (IR504, IR64, Azucena and Zhonghua 11) on the β- and α-diversity of the rhizosphere communities of bacteria, fungi and nematodes as assessed by an adonis test for the structure (including a random effect for the block), the betadisper function from the package vegan for the dispersion, and an anova on a generalized linear mixed model of the abundance with a Poisson distribution for the richness or a gaussian distribution for the Shannon index (including a random effect for the block). Significativity codes for p: *** if < 0.001, ** if < 0.01, * if < 0.05, "NS" if non-significant.

community, again, toward CA.

Second, the effects of the communities on the α-diversity were more contrasted. The microbial richness was higher under CA (Fig. 3E, chisq = 7.25 with $p < 0.01$ for bacteria, Fig. 3G, chisq = 146.83 with $p < 0.001$ for fungi). There were respectively about 3% and 38% more ESVs in the bacterial and fungal communities under CA than under CT. A similar trend was observed in the nematofauna (Fig. 3I) with 7% more families under CA. The microbial richness was also influenced by the variety (Fig. 3D, chisq = 64.79 with $p < 0.001$ for bacteria, and Fig. 3F, chisq = 9.06 with $p < 0.05$ for fungi). There was an interaction between the two effects for bacteria (chisq = 137.50 with $p < 0.001$, due to IR504 that increased richness whereas IR64 reduced it under CA) and for fungi (chisq = 26.70 with $p < 0.001$, with Azucena showing the highest difference between CA and CT whereas IR64 and Zhonghua 11 showed the smallest). The Shannon index for fungi was higher under CA (Fig. 3M, chisq = 5.81 with $p < 0.05$, +11%) and for nematodes (Fig. 3O, chisq = 3.86 with $p < 0.05$, +5%). The Shannon index for nematodes was also impacted by the variety (Fig. 3N, chisq = 13.26 with $p < 0.01$).

3.4. Modified differential abundances of taxa and trophic groups under CA

The effects of the cropping system on the relative abundance of the taxa are presented in Fig. 4 (effect of the practices) and Fig. S4 (effect of the variety). In the bacterial community, 14/42 phyla were impacted by the practices: the relative abundance of *Armatimonadota* (+28%, $p < 0.05$), *FCPU426* (+37%, $p < 0.05$) and *Verrucomicrobiota* (+30%, $p < 0.001$) was higher under CA while the relative abundance of *Chloroflexi* (−43%, $p < 0.001$), *Cyanobacteria* (−61%, $p < 0.01$), *Fibrobacterota* (−75%, $p < 0.001$), GAL15 (−82%, $p < 0.05$), *Hydrogenedentes* (−75%, $p < 0.05$), *Latescibacterota* (−77%, $p < 0.001$), *MBNT15* (−61%, $p < 0.001$), *Myxococcota* (−23%, $p < 0.05$), *Nitrospirota* (−75%, $p < 0.001$), *RCP2–54* (−75%, $p < 0.01$) and *Spirochaetota* (−31%, $p < 0.01$) was lower under CA. We found an effect of the variety on *Chloroflexi* (Azucena < IR504 < Zhonghua 11 < IR64, $p < 0.001$), *Fibrobacterota* (Azucena < IR64 < Zhonghua 11 < IR504, $p < 0.05$) and *MBNT15* (IR64 < Zhonghua 11 < IR504 < Azucena, $p < 0.05$). In the fungal community, 6/13 phyla were impacted by the practices: the relative abundance of *Ascomycota* (+109%, $p < 0.001$), *Blastocladiomycota* (+392%, $p < 0.05$), *Glomeromycota* (+329%, $p < 0.01$), *Monoblepharomycota* (+540, $p < 0.01$) was higher under CA while the relative abundance of *Mucoromycota* (−41%, $p < 0.01$) and *Rozellomycota* (−65%, $p < 0.001$) was lower under CA. We observed an effect of the variety on *Kickxellomycota* (Zhonghua 11 = IR504 < Azucena < IR64, $p < 0.05$). Among the nematofauna, 12/31 families were impacted by the practices: the relative abundance of *Achromadoridae* (+582%, $p < 0.01$), *Anatonchidae* (absent using CT, $p < 0.05$), *Aphelenchoididae* (+176%, $p < 0.05$), *Belondiridae* (absent using CT, $p < 0.05$), *Cephalobidae* (+93%, $p < 0.01$), *Qudsianematidae* (+77%, $p < 0.001$), *Qudsianematidae unsure* (+340%, $p < 0.001$) and *Rhabdolaimidae* (+364%, $p < 0.001$) was higher under CA while the relative abundance of *Ironidae* (−60%, $p < 0.001$), *Leptolaimidae* (−75%, $p < 0.001$), *Pratylenchidae* (−92%, $p < 0.01$) and *Prismatolaimidae* (−69%, $p < 0.001$) was lower under CA. We observed an effect of the variety on *Anatonchidae* (absent in IR504 and IR64, Azucena < Zhonghua 11, $p < 0.05$) and *Ironidae* (IR64 < Zhonghua 11 < Azucena < IR504, $p < 0.05$).

Differential abundance testing (Fig. 5) revealed contrasted taxonomic enrichment profiles depending on the rhizosphere communities. In the communities of bacteria and nematodes, respectively 53% and 64% of the features (term refering to bacterial ESVs, fungal ESVs or nematode families) were enriched under CA whereas in the community of fungi, 65% of the features were enriched under CT (Table 3). Some bacterial ESVs (Fig. 5A) e.g., *Methylocystis* spp., *Bacillus* spp., *Opitutus* spp. and *Geotalea* spp., were enriched in only one variety under one type of practice. Other bacterial ESVs, e.g., *Candidatus Koribacter* and *Bryobacter* spp., were enriched in several varieties under both types of practices. The remaining ESVs had stronger signatures of the effect of practices because they were enriched in several varieties under only one type of practice, e.g., *Aquicella* spp. under CT, *Citrifermans* spp. and *Acidibacter* spp. under CA. All fungal ESVs (Fig. 5B) were also enriched under one type of practice or the other, e.g., *Moeszimyces* spp. under CT or *Gibberella* spp. under CA, except for unclassified *Rozellomycota*, which displayed a particular pattern: fungal ESVs were highly enriched under CT in all varieties except Zhonghua 11, in which two ESVs were enriched under CA. In the community of nematodes (Fig. 5C), the signatures of all enriched taxa were even stronger: 18 families were exclusively enriched under CA and 10 were exclusively enriched under CT. Overall, slightly more features were enriched under CA than under CT (Table 3, 140:126). Different taxonomic enrichment profiles were also influenced by the variety. Zhonghua 11 was the only variety that constantly had more enriched features under CA than under CT (total 57%). Conversely, Azucena had more enriched features under CT than under CA (total 59%).

Some bacterial functions related to the decomposition of relatively small (Fig. 4D) or large molecules (Fig. S5A) were sensitive to the type of practice: taxa putatively associated with nitrification (+665%, $p < 0.01$), chitinolysis (+443%, $p < 0.05$) and ureolysis (+101%, $p < 0.05$) were more abundant under CA, while those associated with hydrocarbon degradation (−56%, $p < 0.001$), methanol oxidation (absent under CA, $p < 0.001$), methanotrophy (−57%, $p < 0.001$) and respiration of sulfur compounds (−53%, $p < 0.01$) were less abundant under CA. Only three of the enriched bacterial ESVs were assigned to a functional guild (Fig. 5A): one to methanotrophy enriched using CT (*Methylocystis* spp.) and two to nitrate reduction enriched using CA

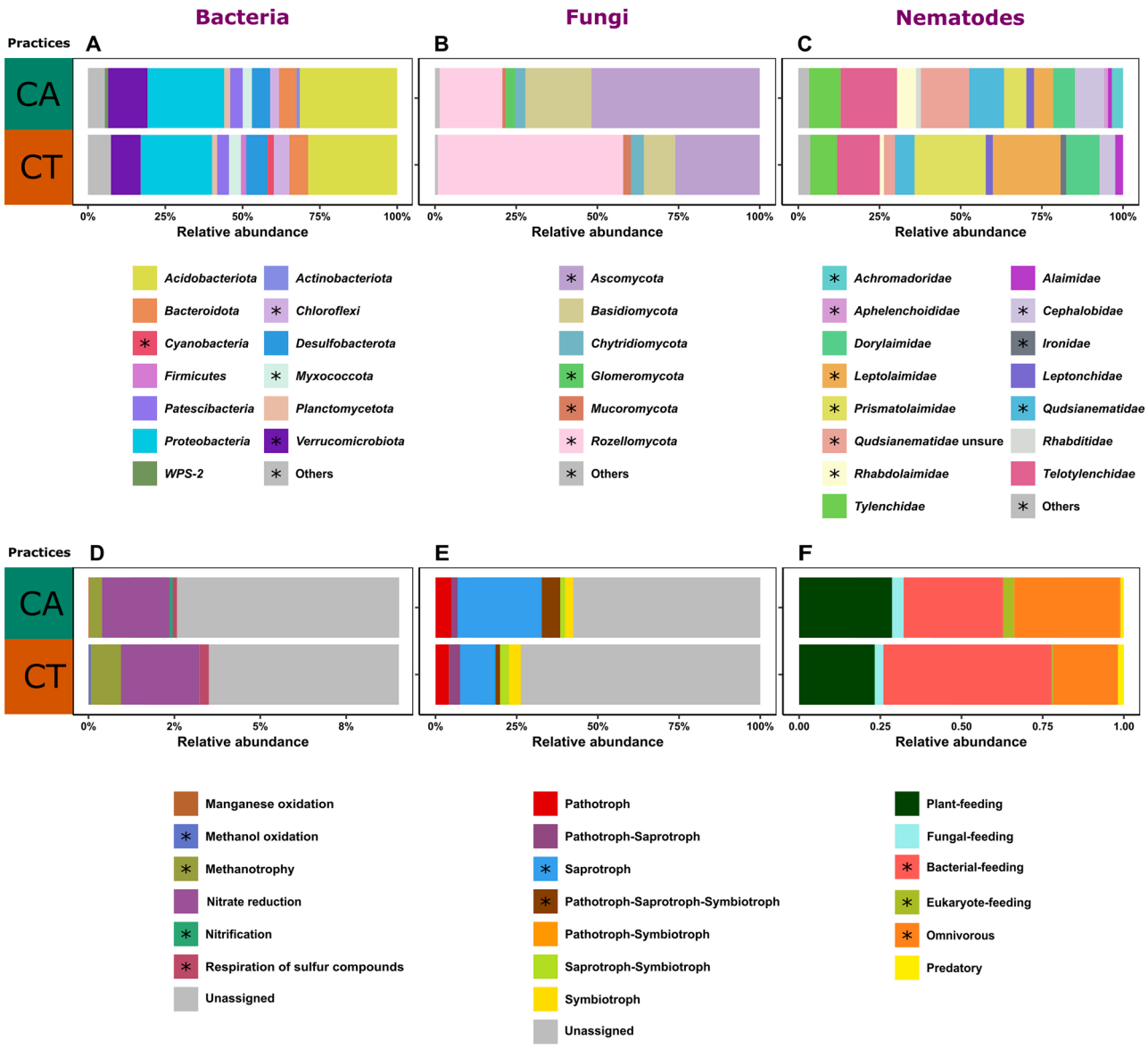

Fig. 4. Relative abundance of taxa (A, B and C) and functional guilds (D, E and F) in the communities of bacteria (A and D), fungi (B and E) and nematodes (C and F) in the rhizosphere of rice varieties (IR504, IR64, Azucena or Zhonghua 11) managed under conventional tillage (CT) or conservation agriculture (CA). Taxa at phylum level (A and B) or family level (C). "Others" had a relative abundance of < 1% each. Features were assigned to either ecological functions from the FAPROTAX database (D), trophic modes from the FunGuild database (E) or trophic groups from the Nemaplex database (F). Asterisks indicate effects of the practices on taxonomic or functional guilds with a $p < 0.05$. Effects of the variety are shown in Fig. S4. Alternative guilds for bacteria are shown in Fig. S5.

(*Azospira* spp. and *Opitutus* spp.). Some fungi putatively associated with trophic modes were relatively more abundant under CA (Fig. 4E): pathotrophs-saprotrophs-symbiotrophs (+251%, $p < 0.001$) and saprotrophs (+164%, $p < 0.01$). Five of the enriched fungal ESVs were assigned to a trophic mode (Fig. 5B): one to pathotrophy enriched under CT (*Moesziomyces* spp.), two to saprotrophy enriched under CA (*Rhizophlyctis rosea* and *Xenomyrothecium tongaense*) and two to pathotrophy-saprotrophy-symbiotrophy enriched using CA (*Saitozyma flava* and *Gibberella intricans*). In the nematofauna (Fig. 4F), the relative abundance of unicellular eukaryote-feeders (+582%, $p < 0.01$) and omnivorous nematodes (+68%, $p < 0.05$) was higher under CA at the expense of bacterial-feeders (−36%, $p < 0.05$). The enriched families (Fig. 5C) were assigned to one plant-feeder enriched under CT (*Psilenchidae* spp.), seven bacterial-feeders enriched under either CT (*Leptolaimidae* spp., *Prismatolaimidae* spp., *Alaimidae* spp. and *Panagrolaimidae* spp.) or CA (*Cephalobidae* spp., *Rhabditidae* spp. and *Rhabdolaimidae* spp.), two fungal-feeders enriched under CA (*Aphelenchoididae* spp. and *Leptochidae* spp.), one unicellular eukaryote-feeder enriched under CA (*Achromadoridae* spp.), four omnivorous feeders enriched under CT (*Ironidae* spp. and *Dorylaimidae* spp.) or CA (*Qudsianematidae* spp. and unsure *Qudsianematidae* spp.).

3.5. Shift in the soil food web indices and structural guilds under CA

Nematofaunal indices revealed higher enrichment index (EI) ($24.2 \pm 18.5 > 10.4 \pm 6.8$, $p < 0.05$), structural index (SI) ($91.4 \pm 4.0 > 85.8 \pm 3.7$, $p < 0.001$) and maturity index (MI) ($3.3 \pm 0.2 > 3.0 \pm 0.1$, $p < 0.001$), and a lower index of organic matter decomposition (IVD) ($89.6 \pm 8.0 < 95.1 \pm 2.9$, $p < 0.01$) under CA than under CT. The higher enrichment and structure indices of the food web under CA are visible in Fig. S6A. The structural guilds of the nematode families (Fig. S6B) revealed a lower relative abundance of early successional opportunists (cp3, −32%, $p < 0.05$), and a higher relative abundance of species with intermediate succession and sensitivity to disturbance (cp4,

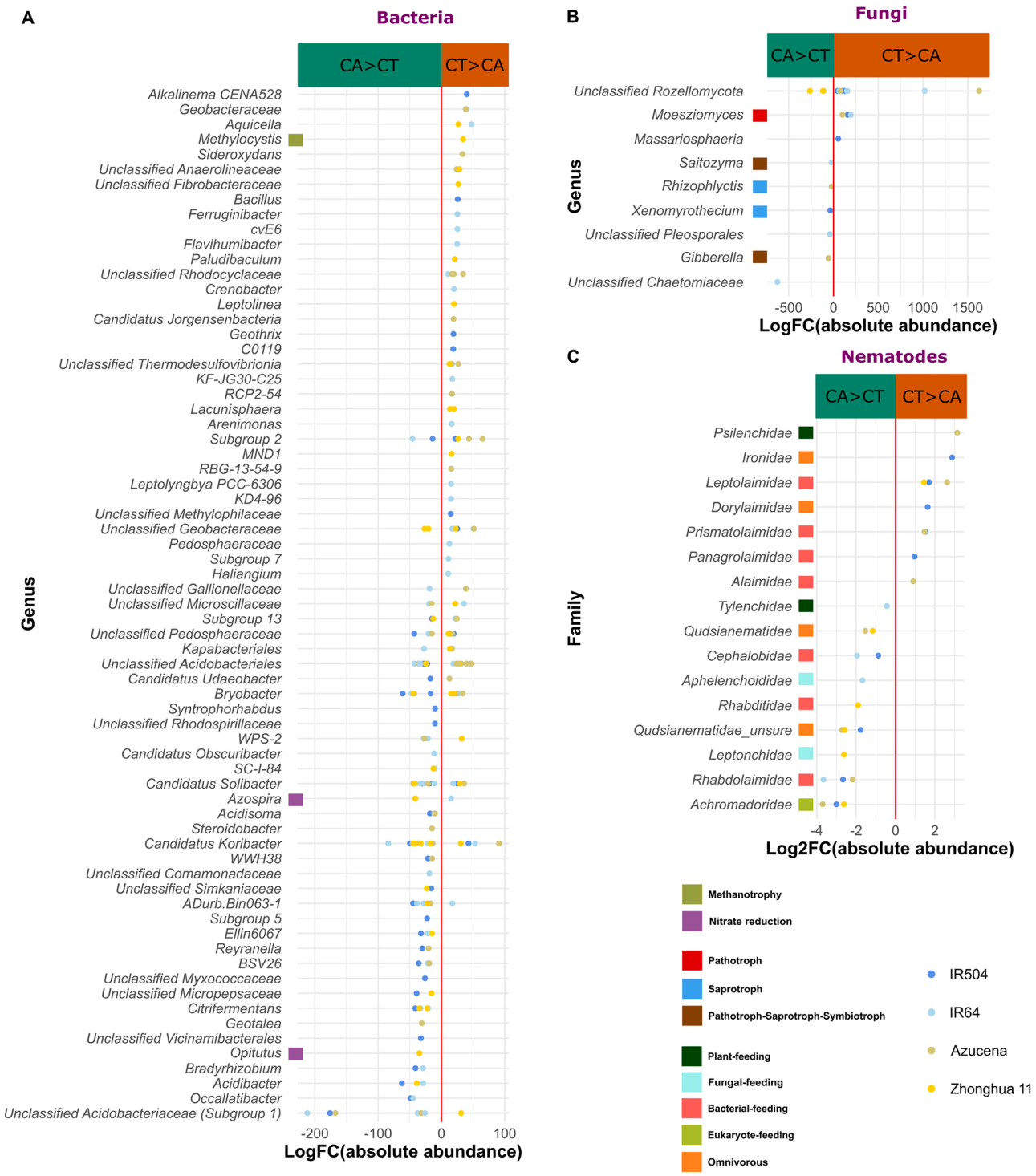

Fig. 5. Enrichments of bacterial (A), fungal (B) and nematode (C) features grouped at genus (A and B) or family (C) levels in the rhizosphere of the four rice varieties (IR504, IR64, Azucena or Zhonghua 11) managed under conventional tillage (CT) or conservation agriculture (CA). Colored squares indicate the functional guilds if assigned. The enrichments ($p < 0.05$) were assessed on features present in at least 25% of the samples for each variety with the package *DAtest*. Features without affiliation at genus (A and B) level are named "Unclassified" followed by the highest assigned taxonomic level.

+45%, $p < 0.05$) and long-lived and species highly sensitive to disturbance (cp5, +409%, $p < 0.01$) under CA.

3.6. Correlations between the PPN abundance and soil abiotic and biotic variables

Correlations were found between the reduction in PPN abundance and the CA edaphic and biotic signature (Fig. 6). The abundance of *Meloidogyne* spp. In rice roots was correlated with soil chemical properties ($r = -0.49$, $p < 0.01$ with the TKN, and $r = -0.39$, $p < 0.05$ with the CEC), with diversity measurements ($0.4 < r < 0.5$, $p < 0.01$ with the NMDS1 coordinates of the three rhizosphere communities and $r = -0.48$, $p < 0.01$ with fungal richness), and with the food web indices ($r = 0.36$, $p < 0.05$ with the IVD and $r = -0.37$, $p < 0.05$ with the MI). The abundance of both phytoparasitic genera including all PPN eggs was also correlated with the same variables, in addition to the NMDS2

Table 3
Differential abundance of bacteria, fungi, and nematodes in the rhizosphere of four rice varieties under the two agricultural practices.

	Bacteria	Fungi	Nematodes	Total
IR504	33:15 (48)	1:7 (8)	4:5 (9)	38:27 (65)
IR64	37:33 (70)	3:4 (7)	5:0 (5)	45:37 (82)
Azucena	21:31 (52)	2:4 (6)	4:4 (8)	27:39 (66)
Zhonghua 11	23:22 (45)	2:0 (2)	5:1 (6)	30:23 (53)
Total	114:101 (215)	8:15 (23)	18:10 (28)	140:126 (266)

Summary of the differential abundance testing on bacterial, fungal and nematode features in the rhizosphere of four rice varieties (IR504, IR64, Azucena or Zhonghua 11) managed under a type of conventional tillage (CT) or conservation agriculture (CA). Number of enriched features under CA versus under CT (CA:CT) and total numbers of features (in parenthesis). The enrichments were assessed on features present in at least 25% of the samples for each variety with the package DAtest.

coordinates of the bacterial community ($r = 0.37$, $p < 0.05$), but without the fungal richness and the food web indices (although $r = -0.34$, $p = 0.055$ with the MI). The abundance of *Hirschmanniella* spp. was correlated with other variables that were only linked to the nematofauna: the total abundance of PPNs in the rhizosphere ($r = 0.39$, $p < 0.05$), the Shannon index ($r = -0.39$, $p < 0.05$) and the EI ($r = 0.39$, $p < 0.05$). Correlations were also found between the reduction in PPN abundance and the relative abundance of functional guilds (Fig. S7). The abundance of *Meloidogyne* spp. was correlated with the abundance of omnivorous nematodes ($r = -0.36$, $p < 0.05$). The abundance of both phytoparasitic genera including all PPN eggs was also correlated with the abundance of omnivorous ($r = -0.40$, $p < 0.05$), in addition to the abundance of saprotrophic fungi ($r = -0.44$, $p < 0.05$) and predatory nematodes ($r = 0.36$, $p < 0.05$).

4. Discussion

In this study conducted on an irrigated lowland rice field, we observed that CA improved the soil quality (+110% of SOC, +83% of TKN, +34% of available P, +10% of exchangeable K, +30% for the CEC), increased the biodiversity (richness: +3% for bacteria and +38% for fungi; Shannon index: +11% for fungi and +5% for nematodes), modified the relative abundances of functional guilds (notably +164% of potentially saprotroph fungi and +665% of potentially nitrifying bacteria, −37% of bacterial-feeding nematodes and +68% of omnivorous nematodes), allowed the maturation of the soil food web (+9% for the maturity index, +132% for the enrichment index and +7% for the structure index) and reduced the abundance of PPNs in the rhizosphere (−64% of *Meloidogyne* spp. in roots and −92% *Hirschmanniella* spp.). Some taxa were enriched under either CA (e.g., one pathotrophic fungus) or under CT (e.g., two saprotrophic fungi) and the varieties also displayed different enrichment patterns. The analysis of the structural guilds revealed that there were fewer early successional opportunists nematodes (−32% cp3) and more persistent nematodes (+45% cp4 and +409% cp5) under CA. We also found correlations associated with the abundance of PPNs, notably between the reduction in *Meloidogyne* spp. abundance in roots and improved soil variables (TKN with $r = 0.49$ and CEC with $r = 0.39$), increased fungal richness ($r = 0.48$), and the decomposition and maturation indices ($r = -0.36$ and 0.37, respectively) of the soil food web.

4.1. The reduction in PPN abundance was observed seven years after the transition to CA

Two PPN species were identified in rice roots in this field located in Stung Chinit: *Meloidogyne graminicola* (present at all developmental

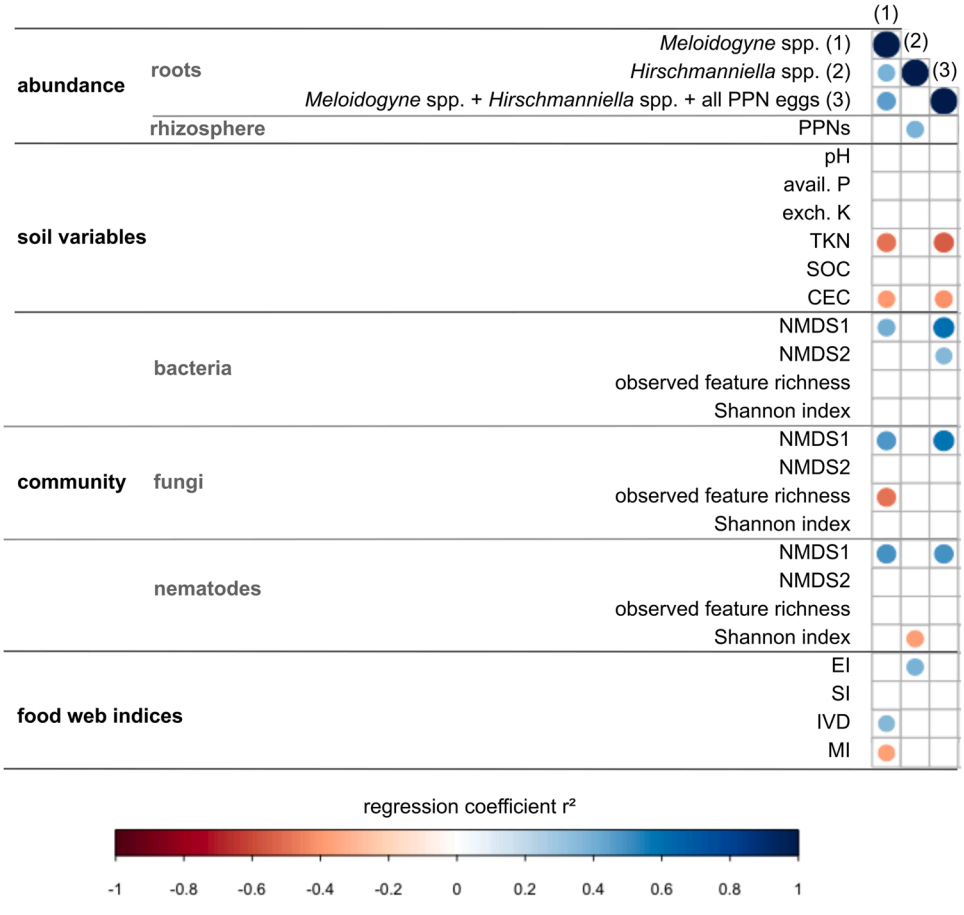

Fig. 6. Heatmap of correlations ($p < 0.05$) linking the abundance of PPNs with soil variables, diversity measurements of the rhizosphere communities and food web indices (EI; enrichment index, SI; structural index, IVD; index of organic matter decomposition and MI; maturity index) associated with the four rice varieties (IR504, IR64, Azucena or Zhonghua 11) managed under conventional tillage or conservation agriculture. Complementary heatmap of correlations between the abundance of PPNs and the abundance of functional guilds in Fig. S7.

stages) and *Hirschmanniella mucronata* (present at the tillering and milky stages) in 2014 and 2015 (Suong et al., 2019). At that time, a few years after the conversion from CT to CA, the abundance of *Meloidogyne graminicola* and *Hirschmanniella mucronata* was about seven times higher under CA than under CT. In the present work, we collected the samples at the tillering stage and extended our investigation to the genus level of these species. For a broader view of the dominant PPNs in this field, we counted the PPNs belonging to the *Meloidogyne* and *Hirschmanniella* genera in addition to the eggs of all PPNs. Our results showed the opposite trend in 2018: the total number of PPNs (*Meloidogyne* spp. + *Hirschmanniella* spp. + the eggs of all PPNs) was about nine times lower under CA than under CT. Moreover, the abundance of the PPNs studied was lower under CA in 2018 (65 PPNs/g of roots) than it was in 2014 or 2015 (364 PPNs/g of roots on average). Despite the higher pressure due to the PPN infection in 2014 and 2015, the rice yield was maintained in both years (Suong et al., 2019). In the present study, we focused on the effects of the components of the cropping system on the rhizosphere communities that might benefit plant health and showed that, after seven years, the pressure from PPNs was lower due to the practices that improved crop health via enhanced soil fertility and biodiversity.

It has been suggested that practices affect the nematode community much more than the crop (Neher et al., 1999; Berkelmans et al., 2003). However, the choice of the varieties impacted the PPN population in the roots. This was particularly clear for *Meloidogyne* spp. possibly because they are sedentary nematodes and thus have a closer relationship with the plant, and also because our varieties differed in their susceptibility to *M. graminicola*. The Zhonghua 11 variety, that is resistant to the infection by *Meloidogyne* spp. (Phan et al., 2018), showed the lowest abundance of PPNs, whereas the Azucena variety was the most susceptible to *Meloidogyne* spp. in our study. Meanwhile, the abundance of *Hirschmanniella* spp. in roots was only slightly impacted by the tested practices, possibly because the biological cycle of these migratory nematodes makes them less affected by tillage, no-tillage and the use of cover crops. Nonetheless, under CA, *Hirschmanniella* spp. were less abundant in the rhizosphere (−92% *Pratylenchidae* that were only represented by *Hirschmanniella* spp.) which is in accordance with some previous studies, including a 12-year experiment under low-input and organic management systems (Berkelmans et al., 2003), and in another seven-year experiment under a similar type of CA in Cambodia (Beesa et al., 2021).

CA practices substantially modified rhizosphere nematofauna by generating a distinct community structure associated with a higher diversity. Another study also showed that reduced tillage (but not organic matter input) increased nematode diversity and the stability of the food web in long-term field experiments in Europe (Bongiorno et al., 2019). In particular, a study by Berkelmans et al. (2003) showed that agricultural practices modified the nematofauna by modulating their trophic levels. In our study, the relative abundance of plant feeders was not significantly impacted under CA but other trophic groups and the structural guilds were modified (notably more omnivorous and more cp4 and 5). Berkelmans et al. (2003) reported that although the differences observed could disappear after a short disruptive management (i.e., tillage), the nematofauna then stabilized over time and regained its original structure at the end of the 12-year long experiment. Since nematodes have key positions in the food web, shifts in their community are generally also associated with restructuring of other soil communities.

4.2. Enrichment of soil resources triggered a bottom-up effect in the food web

Here, we validated our hypothesis that CA benefited the soil food web in our rice field in Stung Chinit. The mulch of cover crops under CA (first trophic level) was a source of organic matter (SOC) and nutrients (NPK) for the microbial decomposers (second trophic level). Improved soil quality associated with increased richness and diversity (especially fungal) restructured the microbial communities in the rhizosphere. Previous studies also showed that a shift to CA has a major effect on soil biodiversity and functions (Chabert and Sarthou, 2017). Long-term no-tillage associated with organic inputs (Wang et al., 2017) or even cover crops alone (Wang et al., 2020) enhance the diversity and stability of the soil microbiota, although this may depend on the cropping system (Kim et al., 2020). Consequently, farming systems such as CA, can improve soil quality by increasing the diversity and abundance of functional guilds (Kibblewhite et al., 2008). In the communities under CA, there was possibly more nitrification due to an enrichment of bacteria such as *Azospira* spp. (Park et al., 2020) and *Opitutus* spp. (Chin et al., 2001) and more saprotrophy due to enrichment of fungi such as *Rhizophlyctis rosea* (James et al., 2006) and *Xenomyrothecium tongaense* (Sterkenburg et al., 2018). The latter species belongs to *Ascomycota* and can play an active role in breaking down plant biomass (Ma et al., 2013; Challacombe et al., 2019).

The changes observed in the bacterial and fungal communities under CA in turn structured populations of fungal- and bacterial-feeding nematodes (third trophic level). Fungal-feeders are generally less abundant than bacterial-feeders in highly disturbed soil systems such as conventional agricultural soils (Villenave et al., 2009b). Soil disturbances such as tillage favor a nematode community dominated by less sensitive, opportunistic and fast-growing bacterial feeders (Ferris et al., 1996; Yeates et al., 2003). In this study, we observed an increase in the fungal- to bacterial-feeder ratio under CA, as revealed by the modified relative abundances and the lower IVD. This measure of primary organic matter decomposition implies that under CA, decomposition was mainly driven by fungal activity rather than by bacterial activity, as already reported under low-input and organic management systems (Berkelmans et al., 2003). In our study, the structure and diversity of the fungal community were the most affected by the practices, which could be due to their particular sensitivity to tillage, especially for mycorrhizal fungi (Gupta et al., 2019) such as *Glomeromycota* spp.

Next, at the fourth trophic level of the soil food web, we observed relatively more omnivorous nematodes under CA. We also observed more eukaryote-feeding nematodes, but in our study, this trophic group was only represented by one family (*Achromadoridae* spp.) and could have been grouped with omnivorous and predatory nematodes (Villenave et al., 2009b). Nonetheless, the abundance of such rare nematodes could be linked to the higher diversity of nematofauna under CA and possibly represent additional soil functions. Interestingly, another study showed that increased organic resources may cascade up the food chain and affect higher trophic levels up to macro-invertebrates, after 14 years of CA in a field with wheat as the main crop (Henneron et al., 2014). Similarly, a study revealed that omnivorous nematodes were more abundant after six years of no-tillage in a soybean field, and that the structure and maturity indices were higher than in the fields under conventional tillage (Okada and Harada, 2007).

Finally, we found a more advanced maturity of the whole soil food web under CA. Changes in the structural guilds resulted in a more enriched and more stable food web. This observation is based on the lower abundance of early successional opportunists nematodes (cp3), and the higher abundances of species with intermediate succession and disturbance sensitivity (cp4) and long-lived intolerant species (cp5). In Berkelmans et al. (2003), the SI and EI were also lower under one type of CT than under low-input and organic management systems. The ban on tillage and the use of cover crops have already been shown to increase enrichment and structure indices and reduce the IVD, with variable effects depending on the type of cover crop used (Ito et al., 2015b). Two families of cp3 bacterial-feeders (i.e., *Leptolaimidae* spp. and *Prismatolaimidae* spp.), one family of cp4 predators (i.e., *Anatonchidae* spp., absent using CT) and one family of cp5 omnivores (i.e., *Qudsianematidae* spp.) significantly contributed to these changes in our study. Finally, due to the enrichment of soil basal resources and avoidance of soil disturbance, CA enabled some species to inhabit the soil and enabled the food web to reach maturity. Another study also found that systems with direct seeding harbor fewer opportunists and a more complex nematofauna,

including taxa that are sensitive to perturbations, than systems that include tillage (Villenave et al., 2009a). Such mature soil can be "suppressive", meaning that there are sufficient predators of various kinds in the food web to reduce populations of opportunistic species (Ferris et al., 2001).

4.3. Mechanisms of potential PPN suppression in the field

Enrichment of soil resources (e.g., SOC and NPK) was correlated with a reduction in PPN abundance in plant roots suggesting that the improvement in soil quality due to agricultural practices negatively affected PPN population. The reduced abundance of *Meloidogyne* spp. in roots was correlated with the increase of MI and relative abundance of omnivorous nematodes. Similarly, Berkelmans et al. (2003) reported that the suppression of *M. javanica* was correlated with increases in EI and SI. The reduced abundance of *Hirschmanniella* spp. in the rhizosphere also suggests that the CA plot was suppressive against these PPNs.

Based on these correlations and on the literature, we propose that the suppression of PPNs observed under CA is due to both direct and indirect competition. Direct competition can involve antagonistic microbes and omnivorous or predatory (generalist or specialist) nematodes. Predatory organisms from high trophic levels in soil food webs can play a role in suppressing plant parasites (Devi and George, 2017). For example, a study showed that the top-down soil suppressiveness of a parasitic nematode, *Meloidogyne incognita*, was related to the predator/prey ratio and to the prevalence of predatory nematodes (Sánchez-Moreno and Ferris, 2006). Another study of the transition from CT to CA in an upland rice field showed that, following an increase in SOC, six years were required for predatory nematodes to appear and to play an active role in biocontrol (Ito et al., 2015a). This delay is comparable to the time needed in the Stung Chinit field to show a reduction in PPN infection. In the rhizosphere under CA, we indeed observed more omnivorous nematodes such as *Qudsianematidae* spp., i.e., generalist predators able to feed on the microbiota and microfauna, and specialist predators such as *Anatonchidae* spp. (absent under CT) and *Mononchidae* spp. that feed only on the microfauna (Khan and Kim, 2007). Interestingly, species of *Qudsianematidae* have been described to prey on *Hirschmanniella oryzae* (Bilgrami and Gaugler, 2005). Omnivorous and predatory nematodes could be responsible for the top-down regulation of *Hirschmanniella* spp. in the rhizosphere in our study. In contrast, Henneron et al. (2014) found no increase in predators perhaps because the conventional field was not tilled in the sampling year. All these results underline the importance of avoiding tillage and of providing a continuous supply of organic inputs through the use of cover crops to allow the soil food web to mature and to create a favorable niche for persistors-predators.

Microbes may also play a direct or indirect role as biological control agents of PPNs, as suggested by the negative correlation between *Meloidogyne* spp. abundance in roots and fungal richness. Some fungi are known to be antagonists of PPNs including the nematode-trapping fungi *Arthrobotrys* spp., *Dactylellina* spp. or *Mortierella* spp., the endoparasitic fungus *Catenaria* spp. and the egg and female parasitic fungi *Purpureocillium* spp., *Dactylella* spp. or *Trichoderma* spp. (Topalovic et al., 2020) that were all found in our samples. Such fungi can impact PPN populations specifically or generally (Jaffee et al., 1997; Jaffee and Strong, 2005; Stirling, 2014). Indirect mechanisms can involve microbes able to induce systemic resistance in the plant. For example, *Glomeromycota* spp., which were enriched under CA, are obligate associates of plants and may be able to protect tomato and pepper against *M. incognita* (Rodriguez-Heredia et al., 2020). Other arbuscular mycorrhizal fungi such as *Glomus mosseae* have also been shown to reduce penetration by -and the life development rate of- *M. incognita* in tomato (Vos et al., 2012). Although soil suppressiveness seems to involve both abiotic and biotic factors, Topalovic et al. (2020) and Watson et al. (2020) have demonstrated that microbes from specific soil may trigger high reductions of root-knot nematode populations. In the rice field in Stung Chinit, CA could have created a favorable environment for the development and plant recruitment of biological control agents to suppress PPNs. Further investigations are now required to fully understand the mechanisms of soil suppressiveness and their contribution to crop health and productivity (Trivedi et al., 2020) in this field.

5. Conclusions

An experiment was conducted in a rice field in Cambodia to monitor the PPN infection under contrasted cropping systems: conservation agriculture (CA: no-tillage and cover crops) versus conventional agriculture (CT: including tillage) using four rice varieties (IR504, IR64, Azucena, Zhonghua 11). We found that after seven years, rice roots were less infected by PPNs under CA. Our data reinforce results of previous studies showing that CA favors soil ecosystem services: no-till cropping systems combined with the use of cover crops increased organic matter inputs above and belowground, and consequently triggered structuring and enrichment of the whole soil food web. We suggest that the food web maturity is associated with the development of soil biota that preys on (e.g., predatory nematodes) or parasitizes nematodes (e.g., nematode-trapping fungi), and promote plant growth and defense (e.g., mycorrhizal fungi). CA resulted in disease suppression. This could have led to the reduction in PPN abundance, especially *Meloidogyne* spp. in roots and *Hirschmanniella* spp. in the rhizosphere. CA relieves parasitic pressure on rice and possibly counterbalances disease outbreaks. Further research is needed to unravel the mechanisms involved in the reduction in PPN abundance. Even though the rice variety is an important component of the cropping system because it provides resistance at the plant level, i.e., resistance to *Meloidogyne graminicola* with Zhonghua 11, the four tested varieties had very little effect on the rhizosphere communities. However, this result requires further investigation into the ability of the varieties to recruit specific microorganisms and to interact with them. Finally, by improving soil quality and crop health, CA is a very promising alternative cropping system to support the transition to more sustainable rice production in South-East Asia. The description of the soil food web in this study provides a snapshot of an agroecosystem that requires more monitoring to evaluate the full potential of CA for the regulation of pest and pathogen populations, and for other services including the support of nitrogen and carbon cycles.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.107913.

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