Mycorrhiza (2021) 31:265–272
https://doi.org/10.1007/s00572-020-01007-0

SHORT NOTE

Diversity and species composition of arbuscular mycorrhizal fungi across maize fields in the southern part of Belgium

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Received: 14 August 2020 / Accepted: 11 November 2020 / Published online: 19 November 2020

Abstract

Arbuscular mycorrhizal fungi (AMF) are key actors among soil microbial inhabitants, forming beneficial associations with most horticultural plants and crops (e.g., maize). For maize, the world most cultivated cereal, data on AMF species diversity in fields is sparse and even totally nonexistent in the southern part of Belgium where maize represents 8% of the cultivated area. In the present study, 14 maize fields in South Belgium under conventional, conversion, or organic management were analyzed for AMF diversity and species composition using 454 pyrosequencing. A large part (54%) of the 49 AMF species observed were unknown or have not been described in the literature. AMF diversity highly varied among fields, with the number of species ranging between 1 and 37 according to the field. A statistically significant effect of management was measured on AMF diversity, with the highest Hill index values (diversity and richness) under the organic management system compared with conventional management or conversion. Our results suggest a positive effects of organic management on AMF diversity in maize. They also highlight the rather high diversity or richness of AMF and the large portion of sequences not yet ascribed to species, thereby emphasizing a need to intensify AMF identification in cropping systems.

Keywords Arbuscular mycorrhizal fungi · Diversity · Maize · 454 pyrosequencing

Introduction

Maize (*Zea mays* L.) is the world's most cultivated cereal crop, with over 1.1 billion tons harvested worldwide in 2018 (FAO 2018 http://www.fao.org/faostat/fr/#data/QC). It mainly is used as livestock feed and as a staple food but also is important for biofuel production (Zerbe 2015) and polymer applications (Berta et al. 2014).

In the southern part of Belgium, maize crops cover 8% of the cultivated area (STATBEL 2017 https://statbel.fgov.be/fr/nouvelles/chiffres-cles-de-lagriculture-2018), with an average yield of 44.9 tons per ha for corn fodder and 12 tons per ha for grain corn, respectively. Maize mostly is cultivated under conventional practices, while organic cultivation represents less than 1% of the total cultivated area (G. Foucart–Centre Indépendant de Promotion Fourragère–https://cipf.be/fr/mais—personal communication). Conventional agriculture largely depends on chemical fertilizers and pesticides as well as other operations such as tillage and monoculture for maximizing yield. These agricultural practices, if not reasonably applied, may significantly affect the abundance, diversity, and species composition of soil microorganisms (Green et al. 2005; Mahmood et al. 2016; Suman et al. 2018) and thus threaten the ecosystem services they offer (Costanza et al. 1997). Thus, for maximizing the functions of microorganisms in agroecosystems, it is important to develop agricultural practices (e.g., absence of pesticides, use of organic fertilizers, and limited tillage as in organic management) preserving or, even better, promoting a beneficial rhizosphere microbiota (Olanrewaju et al. 2019).

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Among the key microorganisms developing in the rhizosphere are arbuscular mycorrhizal fungi (AMF) (Smith and Read 2008). These soil fungi are obligate symbionts forming associations with an estimated 72% of terrestrial plant species (Brundrett and Tedersoo 2018). Their roles in mineral nutrition and water supply of plants (Smith and Read 2008) as well as effects on improving plant resistance/tolerance to abiotic (see review by Plouznikoff et al. 2016) and biotic (see review by Pozo and Azcón-Aguilar 2007; Whipps 2004) stresses have been reported repeatedly.

Although the diversity of AMF is not always low in arable soil (Hijri et al. 2006), the majority of studies reported to date have emphasized the harmful effects of conventional cultural practices (e.g., monoculture, mechanical tillage for weed control, bare fallow, heavy fertilization, application of fungicides) on AMF diversity and abundance (Gosling et al. 2006; Oehl et al. 2003, 2005; Schlaeppi et al. 2016), while the reverse often has been noticed under organic management systems (Verbruggen and Kiers 2010).

Maize is host to AMF with root colonization under field conditions reaching 50 to 80% in some studies (An et al. 2010). Beneficial effects of AMF on maize have been reported on phosphorus (Bhat et al. 2017) and micronutrient (Dias et al. 2018; Kaeppler et al. 2000; Ramírez-Flores et al. 2019; Rocha et al. 2019) acquisition, as well as on increasing tolerance to drought (Boomsma and Vyn 2008; García-González et al. 2016). Few studies, however, have been conducted on AMF diversity in maize fields. In a fertile Chernozem cropland from Central Europe, 36 species belonging to 17 genera were reported (Baltruschat et al. 2019). Furthermore, the work on maize by Verbruggen et al. (2010) has shown that organic management enhances the diversity of AMF when compared with conventionally managed agricultural fields. However, no information is available on AMF diversity and species composition associated with maize crops grown in the Southern part of Belgium.

In the present study, 14 fields of maize cultivated under contrasting agricultural management were analyzed by 454 pyrosequencing with the objective of evaluating the AMF diversity and species composition in maize fields of the southern part of Belgium, a necessary step towards forecasting the integration of these beneficial microorganisms into management practices of maize cultivation.

Materials and method

Sampling location

Root samples were collected in November 2013 from 14 different maize fields located in the southern part of Belgium (Sup Fig. 1). The climate of the region is temperate with annual mean precipitation and temperature of 1191 mm and 8.3 °C, respectively (PAMESEB 2013). Two fields were grown in organic management conditions ((EC) No 834/2007, https://eur-lex.europa.eu/eli/reg/2007/834/oj) (Bure and Wavreille), 1 field (Wanze) was in conversion (i.e., 2 years are required for annual culture before the organic label can be used in the European Union; https://doi.org/10.2861/488634), and the remaining eleven fields were under conventional agricultural management (Sup. Table 1). Soil physico-chemical analyses were done by the "Le centre provincial de l'agriculture et de la ruralité (CPAR)" (Sup Table 1). AMF diversity in maize roots was assessed at harvest by using 454 pyrosequencing. Four plants from each field were selected randomly; therefore, 56 samples were analyzed. The roots were cleaned of soil particles with tap water and stored at − 80 °C before analyses. Samples were used for assessment of AMF diversity and species richness.

DNA extraction

DNA was extracted from the root samples according to Garcés-Ruiz et al. (2017). In brief, ~ 70 mg of dried roots from each sample was ground and the material transferred into a Lysing Matrix E tube from the FastDNA SPIN Kit for Soil (MP Biomedicals, USA). DNA was extracted following the manufacturer's protocol. The DNA integrity was visualized in 1% electrophoresis gel and 5 µl of the product was stained with 100× GelRed™ (Nucleic Acid Gel Stain, Biotium, Belgium). Samples were run at 100 V for 18 min in 0.5× TAE buffer and stored at − 20 °C until further use.

PCR conditions and 454-pyrosequencing

Two PCRs were performed. The first one was made according to Krüger et al. (2009). The amplification spanned a fragment covering the partial SSU, the complete ITS region, and partial LSU rRNA gene. The primer pairs SSUmAf–LSUmAr and SSUmCf-LSUmBr were used. They targeted 1.8 and 1.5 kb regions, respectively. The second PCR was a nested PCR, performed as described by Senés-Guerrero and Schüßler (2016b) in which the product of the first PCR served as template for the second PCR. Nested PCR primer pairs amplified a fragment of around 800 bp from the LSU rRNA gene region. Amplicons were amplified, using fusion primers. Thermal cycling was done in an Eppendorf Mastercycler Gradient (Eppendorf, Germany) with the following conditions for the first PCR: 5-min initial denaturation at 99 °C; 40 cycles of 10-s denaturation at 99 °C, 30 s annealing at 60 °C, and 1 min elongation at 72 °C; and a 10-min final elongation. In the nested PCR, 1 µl of the first PCR product was used in the final reaction (20 µl). The thermal cycling conditions were the same as for the first PCR, except that only 25 cycles were done (Senés-Guerrero and Schüßler 2016a). For each sample, three separate PCRs

were performed, and the products loaded on 1% agarose gel for electrophoresis. Then, PCR replicates for each sample were pooled after confirming a visible band. The pooled products were loaded on 1% agarose to purify with the QIAquick® Gel Extraction Kit (Qiagen, Germany). DNA quantification was performed with the Quant-iTTM Pico-Green dsDNA Assay Kit (Life technologies, USA) following the manufacturer's protocol. The samples were quantified in a fluorometer (Fluoroskan Ascent FL, Labsystem, USA) with the Ascent Software (Louisc, nsku91). According to the results, the samples were diluted until they reached 109 molecules μl^{-1}. The samples were mixed to equimolar concentration. Finally, diluted PCR products were pooled in an equimolar concentration to obtain only one sample. A total of 454 pyrosequencing was done by using 2 XLR GS Junior Sequencing (Nucleomics Core, Leuven Belgium, http://www.nucleomics.be/).

Bioinformatic analyses

Analyses were performed according to Senés-Guerrero and Schüßler (2016a) and Senés-Guerrero and Schüßler (2016b). In an initial step, the sequences were quality-filtered and clustered at 98% to obtain one representative sequence (RS) per cluster. The next step involved phylogenetic placement by evolutionary placement algorithm (EPA) of the RS into a reference phylogenetic tree. The QIIME pipeline (Caporaso et al. 2010) was used for the initial analysis. The parameters to select reads for downstream analyses consisted of reads with no more than 15 ambiguous bases, a maximum length of homopolymer run of 15, a maximum number of 5 primer mismatches, and sequences with a minimum length of 500 bp including the primers. The remaining sequences were clustered at a 98% similarity threshold to obtain RS and to avoid merging of different species in the same cluster (Senés-Guerrero and Schüßler 2016a). After clustering, singletons were removed and the remaining RS were blasted against the NCBI nucleotide database using Blast2GO (Conesa et al. 2005) to identify and remove non-AMF sequences. The remaining RS (with no non-AMF sequences and no singletons) were taken for species delimitation by means of the RAxML EPA with the GTR-GAMMA model performed through a web interface (Berger et al. 2011; Berger and Stamatakis 2011) using a "phylogenetic backbone tree" based on 1.5 kb reference sequences (Krüger et al. 2012) for sequence placement. The branches of the phylogenetic backbone tree show the placement of the short sequences by EPA. To allow comparisons, species were annotated with the same species numbers as used in previous studies (Garcés-Ruiz et al. 2017; Loján et al. 2017; Senés-Guerrero and Schüßler 2016a; Senés-Guerrero et al. 2014). Sequences are available on NCBI SRR12900578, SRR12900579, and SRR12900580.

Statistics analyses

Statistical analyses were performed, using JMP[§] Pro statistical software version 14.0.0 (SAS Inc., Canada). Normality was tested with the Shapiro-Wilk *W* test. For exponential of the Shannon's index, a square root transformation was used, and for inverse of Simpson's concentration index (Simpson's index), a log10 transformation was used to normalize the data. Alpha-diversity (i.e., local diversity) was evaluated by Hill numbers (Oksanen et al. 2016) (H) with $q = 0$ (species richness, H0), $q = 1$ (exponential of Shannon's index, H1), and $q = 2$ (inverse of Simpson's concentration index, H2). Hill's diversity series is an intuitive measure of diversity in which the q order of diversity indicates its sensitivity to species abundance (Battie-Laclau et al. 2019). Hill numbers were compared between agricultural management (conventional, conversion, organic) by one-way ANOVA followed by Tukey post hoc tests. Rarefaction curves were obtained by using the function described by Chao et al. (2016—see https://chao.shinyapps.io/iNEXTOnline/).

Results

From the 14 field samples (Fig. 1), 8.3% of the sequences could not be assigned to AMF after removal of singletons. A total of 79,899 sequences fulfilled the parameters of selection and 46% of the reads could be assigned to species. The reads were clustered at 98% nucleotide identity, a threshold ensuring that no interspecific sequence variants are clustered (Senés-Guerrero and Schüßler 2016b), to obtain 2117 representative sequences (RS). The RS were affiliated to the reference sequence phylogenetic tree (by EPA) with 143 AMF clades interpreted as species. From these, 49 annotated species were detected in the 14 fields (Fig. 1). Twenty-six of these 49 annotated species (accounting for 54% of the reads) were unknown or previously not described in sequence data. Five of them were closely related to identified species but separated at the species level, and one was identified only at the genus level. Curves of species accumulation showed plateaus for eleven fields, indicating that sequencing depth was sufficient to represent the AMF species diversity except for three other fields, Etalle, Wanze, and Hornu, where this was not the case (see Fig. S2).

The 49 species belonged to 15 genera (Fig. 1) with the most diverse being *Rhizophagus* (9 species), *Diversispora* (9 species), *Claroideoglomus* (7 species), and *Funneliformis* (5 species). The 15 genera belonged to 7 of the 12 families of the phylum Glomeromycota: *Acaulosporaceae* (1 genus), *Archaeosporaceae* (1 genus), *Claroideoglomeraceae* (1 genus), *Diversisporaceae* (1 genus), *Gigasporaceae* (4 genera), *Glomeraceae* (6 genera), and *Paraglomeraceae* (1 genus). Two families (*Glomeraceae* and *Paraglomeraceae*)

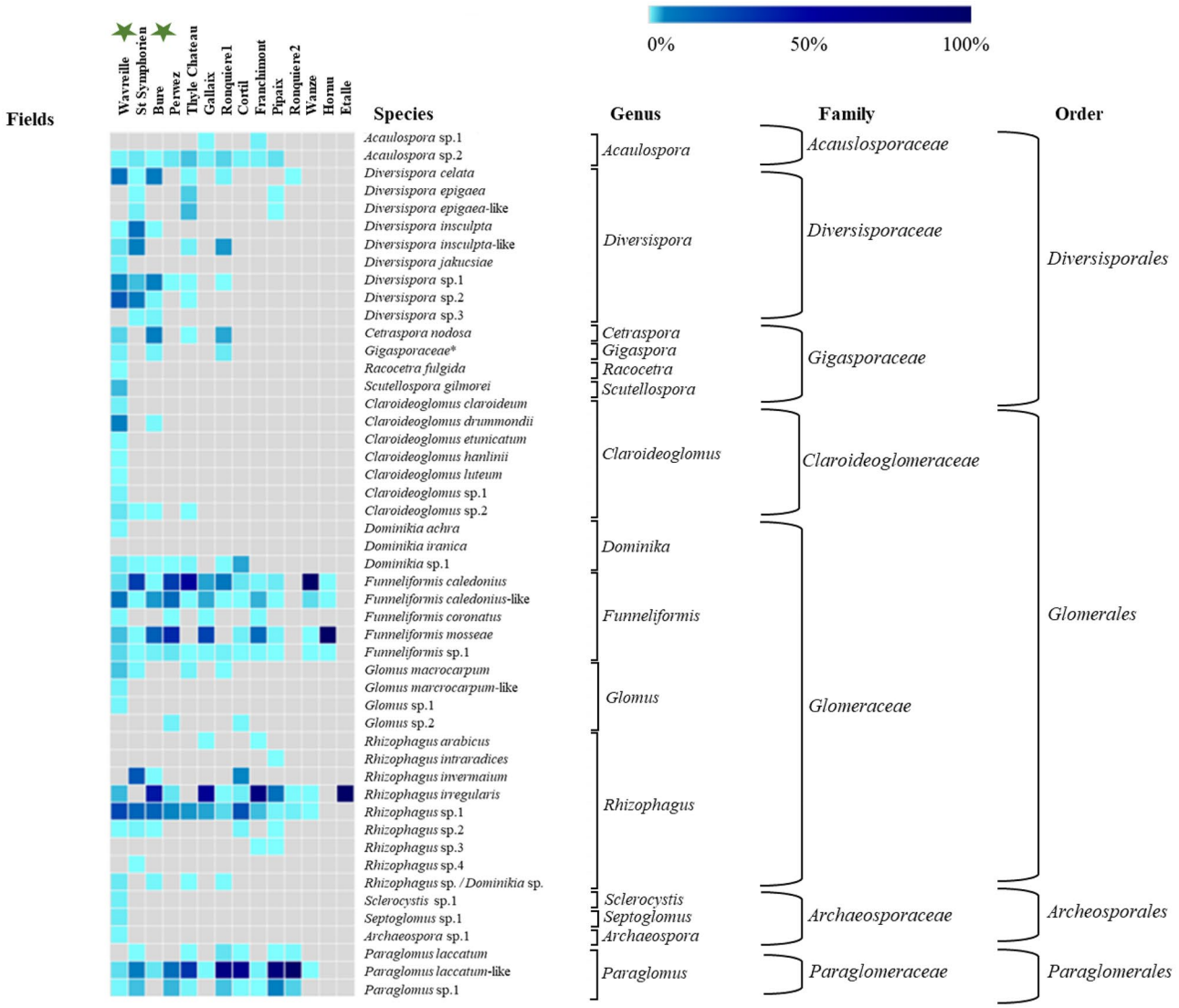

Fig. 1 Arbuscular mycorrhizal fungal (AMF) species communities in 14 fields of south of Belgium. Heat map presenting the % of identified and unidentified species in each field, with columns and rows representing fields and species, respectively. Organic fields (green star), Gigasporaceae (*) either *Scutellospora or Gigaspora*

accounted for most AMF sequences represented by three genera: *Funneliformis*, *Rhizophagus*, and *Paraglomus*. Among the 49 species, four (i.e. *F. caledonius*, *F. caledonius*-like, *F. mosseae*, *Funneliformis* sp., *P. laccatum*-like, and *Rhizophagus* sp.) were present in 12 of the 14 fields. One *R. irregularis* was present in 11 fields and one *Acaulospora* sp. and *F. mosseae* were present in 10 fields. *Acaulospora* sp. were found (three unidentified species) in 10 of the 14 fields and *Claroideoglomus* species also were detected even if mainly in Wavreille, revealing a rather unexpected high diversity for maize cropping systems.

All three Hill indices differed depending on the field (Sup. Table S1). Two fields were grown under organic management, Bure and Wavreille, one was in conversion and the remaining eleven involved conventional management (Sup. Table 1). The highest diversity (i.e., H1 or H2) was measured in Wavreille (H1 = 13.06; H2 = 7.95) and the lowest in Etalle (H1 = 1.00; H2 = 1.00) (Sup. Table 1). Those H1 and H2 indices can be linked to the species richness (H0). Indeed, 37 species (20 unknown accounting for 68% of total species in this field) were observed in Wavreille and only one in Etalle. Half of the fields (Pipaix, Franchimont, Cortil, Ronquiere1, Gallaix, Thy-le-Chateau, Perwez) had a H1 between 2 and 6, four (Ronquiere2, WanzeT3, Hornu, Etalle) were below 2, and 3 were above 6 (Bure, St Symphorien, Wavreille) (Sup. Table 1). Interestingly, two of the most diverse (i.e., high H1) fields were under organic management

(Wavreille H1 = 13.06 and Bure H1 = 6.04) (Fig. 2). The limited number of fields considered in organic or conversion management limit the statistical analyses, but nevertheless, Tukey tests confirmed higher diversity (H1, $P < 0.019$; H2, $P < 0.027$) and richness (H0, $P < 0.027$) in field under organic management compared with conventional management. No differences in Hill indices were evident between fields conventionally managed and the one in conversion.

A high number (i.e., 26) of unknown or undescribed AMF species were detected, accounting for 54% of the AMF sequences. Those species notably belong to the "generalist" genera such as *Funneliformis*, *Rhizophagus*, and *Paraglomus.*

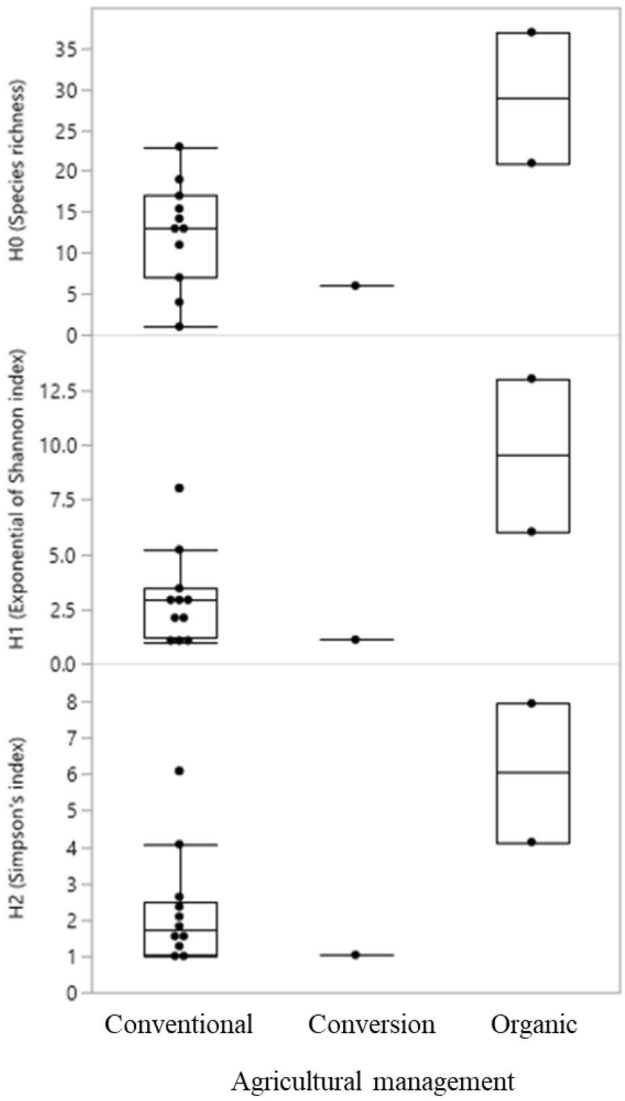

Fig. 2 Local diversity assessed by Hill's indices according to agricultural management presented as box plot around median, with observed values in each field. Lines extending from the boxes indicating variability outside the upper and lower quartiles

Discussion

Our results highlighted the rather high diversity present in maize fields in the South of Belgium (Fig. 1), especially for organic managed (Wavreille and Bure) but also in some conventionally managed (St Symphorien) cropping systems. These results are in accordance with the study of Borriello et al. (2012) reporting a rather high diversity in maize fields in central Italy. Species belonging to the *Glomeraceae* were the main root colonizers, and they co-occurred with *Gigasporaceae* and *Paraglomus* regardless of management practices (Borriello et al. 2012). *Funneliformis*, *Rhizophagus*, and *Paraglomus* species often accounted for a large part of the AMF sequences that we detected and could even be largely dominant as shown in Etalle with 100% of detection due to *R. irregularis* or 99% for *F. mosseae* in Hornu and 98% of *F. caledonius* in Wanze. In our experiment, these species correspond to "typical AMF of arable land" or "AMF generalists" as described in Oehl et al. (2003) and Oehl et al. (2004). *Rhizophagus irregularis* and *R. intraradices* also were found as dominant species in arable soils (Schlaeppi et al. 2016). *Funneliformis* and *Rhizophagus* species each have been shown to account for 29% of sequences detected in maize crops (van Tuinen et al. 2020). We also have observed closely related species, named as "species like," which already have been reported for the generalist *R. irregularis*. Indeed, arable soils and grasslands contain completely different sets of *R. irregularis* when mtLSU haplotypes are analyzed (Börstler et al. 2010).

Agricultural practices are numerous, and the effects of one practice may be counterbalanced by another practice, thus requiring experimental plans with high number of fields and replicates to highlight in a sufficiently clear manner the role of certain practices on AMF diversity. Interestingly, the two organic fields in our study have the highest AMF diversity (H1and H2) and richness (H0) suggesting a possible effect of global practices on diversity (restricted fertilization and pesticide use, crop rotation, cover crops). Wavreille and Bure were under organic management for several years (at least 3 years) notably with grass culture and low phosphorus. Conversion to organic management has been shown by Verbruggen and Kiers (2012) to significantly increase AMF richness over time, and AMF communities of organically managed fields also were more similar to those of natural grasslands than those of fields under conventional management (Verbruggen and Kiers 2010). Organic management might allow the AMF "gene-bank" found just below the depth of ploughing to develop again, increasing the AMF diversity and richness in the top soil (Oehl et al. 2005). In some cases, however, it appears that some AMF taxa were not necessarily

affected by agricultural practices (Higo et al. 2018) and that AMF diversity in maize field plots was primarily influenced by ammonium nitrate fertilization and, to a lesser extent, by tillage (Borriello et al. 2012). However, conventional cultural practices potentially reduce the symbiotic quality of the AMF community (Verbruggen et al. 2015), even if AMF communities of low species diversity still may contain considerable functional heterogeneity (Munkvold et al. 2004). Therefore, it appears difficult to globally explore the effects of agricultural practice on AMF diversity in maize crops, and more research should be conducted to identify what are the trait profiles of AMF genotypes that are lost during agroecosystem establishment/management (Rillig et al. 2019).

The exponential Shannon index (H1) reported on maize generally ranges between 1.63 and 5.59 (Borriello et al. 2012; Jefwa et al. 2012; Miao-Yan et al. 2009; Oehl et al. 2005). Therefore, our results revealed four fields (i.e., Etalle, Hornu, Wanze, Ronquiere2) with low diversity (Sup. Table 1), with maize colonization mainly attributed to highly competitive species (i.e., *R. irregularis*, *F. mosseae*, *F. caledonius*) and one field (Wavreille) with high diversity and rather cryptic species (i.e., *Clareoideoglomus* sp., *Septoglomus* sp., *Archeospora* sp.). The other fields were inside the range of H1 reported in the literature, with AMF communities typically dominated by a single taxon. These dominating taxa have been found to represent on average 40% of the total abundance within a given community (Dumbrell et al. 2010). Phylogenetic analysis of the most abundant taxa across data sets showed that the dominant AMF type in each community was different and not necessarily a widespread generalist (Dumbrell et al. 2010). An explanatory hypothesis is that 'founder AMF' species colonizing plant roots early during ecological succession benefit from more plant-derived carbon than 'latecomers', which would favor founder species growth and spread through the soil and increase their probability of colonizing newly formed roots (Chagnon et al. 2012).

Our molecular approach has been used to assess diversity indices in main crops like potatoes or in forest areas (Garcés-Ruiz et al. 2017, 2019; Loján et al. 2017; Senés-Guerrero and Schüßler 2016a, 2016b; Senés-Guerrero et al. 2014; Taylor et al. 2017) and has allowed identification of a quarter to half of the AMF species (Fig. 1) present in association with crop culture, in those experiments. Together, those measures show that even in soil regularly used for crop production, the proportion of unknown/undescribed AMF species remains rather high. Functional diversity is important for the growth of individual plants and for the composition of plant communities (van Der Heijden et al. 2004); therefore, it appears necessary to identify those unknown or undescribed species and to characterize their functional traits (Chagnon et al. 2012). Indeed, plant growth promotion and phosphorus uptake may differ among AMF species as well as among isolates of a single species (Munkvold et al. 2004). However, most available commercial inocula comprise only a few species (Brito et al. 2018). Our hypothesis is that the unknown/undescribed AMF species are functionally important in natural ecosystems (Oehl et al. 2004; Rillig et al. 2019) and potentially capable of contributing to nutrient use efficiency in cropping systems (Verzeaux et al. 2017).

Conclusion

Nowadays, 334 AMF species have been described (see http://www.amf-phylogeny.com/amphylo_species.html, accessed in Jun 2020). However, results of phylogenetic analyses of sequences of nrDNA extracted from plant roots suggest that fewer than *circa* 10% of existing AMF species in the world are known to date (Błaszkowski et al. 2015). Molecular approaches allow detecting putative cryptic species not yet characterized as morpho-species because they are present in soil as mycelia and not as spores (Borriello et al. 2012; Stefani et al. 2020). In the present study, we depicted the AMF community composition across maize fields in the southern part of Belgium. A relatively high number of AMF species (49) were detected. We measured a significantly higher diversity and richness in fields under organic management compared with conventional management. More than half could not be ascribed to a species or are unknown from the literature. Their symbiotic function and capacity to spread are thus unknown, but it is not excluded that they may have potential for application in conventional or organic cropping systems, thereby requiring their isolation, identification, and testing.

Supplementary Information The online version contains supplementary material available at (https://doi.org/10.1007/s00572-020-01007-0).

Acknowledgments We would like to thank Emmanuel Niyigena and Catherine Rasse of «Support en Méthodologie et Calcul Statistique» (Université catholique de Louvain) for their help with statistical analyses. MC and P-LA received financial support from the Service Public de Wallonie Direction générale opérationnelle de l'Agriculture, des Ressources naturelles et de l'Environnement Direction de la Recherche, under contract No D31-1314.

Authors' contributions MC, SC, GF, and SD conceived the experiments. MC, VM, GM, GF conducted the experiments. CSG conducted the NGS data analyses. P-LA analyzed the results and wrote the manuscript. SC, SD, CSG reviewed the manuscript.

Funding This research was supported by the Direction Générale opérationnelle de l'Agriculture, des Ressources naturelles et de l'Environnement du service public de Wallonie, contract number D31/1314.

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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