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Title: Crop residues in wheat-oilseed rape rotation system: a pivotal, shifting platform for microbial meetings

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Abstract

Crop residues are a crucial ecological niche with a major biological impact on agricultural ecosystems. In this study we used a combined diachronic and synchronic field experiment based on wheat-oilseed rape rotations to test the hypothesis that plant is a structuring factor of microbial communities in crop residues, and that this effect decreases over time with their likely progressive degradation and colonization by other microorganisms. We characterized an entire fungal and bacterial community associated with 150 wheat and oilseed rape residue samples at a plurennial scale by metabarcoding. The impact of plant species on the residue microbiota decreased over time and our data revealed turnover, with the replacement of oligotrophs, often plant-specific genera (such as pathogens) by copiotrophs, belonging to more generalist genera. Within a single cropping season, the plant-specific genera and species were gradually replaced by taxa that are likely to originate from the soil. These changes

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occurred more rapidly for bacteria than for fungi, known to degrade complex compounds. Overall, our findings suggest that crop residues constitute a key fully-fledged microbial ecosystem. Taking into account this ecosystem, that has been neglected for too long, is essential, not only to improve the quantitative management of residues, the presence of which can be detrimental to crop health, but also to identify groups of beneficial micro-organisms. Our findings are of particular importance, because the wheat-oilseed rape rotation, in which no-till practices are frequent, is particularly widespread in the European arable cropping systems.

Keywords

community succession, microbial diversity, oilseed rape, residue microbiota, wheat

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Background

Crop residues are an essential living element of agricultural soils. Smil [1] stressed that they "should be seen not as wastes but as providers of essential environmental services, assuring the perpetuation of productive agrosystems". When left in the field in the period between two successive crops, rather than being buried immediately, crop residues contribute to the formation of soil organic carbon, improve soil structure, prevent erosion, filter and retain water, reduce evaporation from the soil surface, and increase the diversity and activity of micro-organisms in the ground [2]. No-till practices are becoming increasingly widespread, as they take advantage of these attributes [3]. However, such practices are often considered likely to increase the risk of disease epidemics [4–6]. Indeed, several leaf-, stem-, head-, and fruit-infecting micro-organisms, classified as "residue-borne" or "stubble-borne" pathogens, are dependent on host residues for survival during the period between successive crops and for the production of inoculum for their next attack [7, 8]. The epidemiological contribution of residues as an effective source of inoculum is well-established but difficult to quantify [e.g. 9] and generalise, because the nature of survival structures depends on the biology of the species. The situation is rendered even more complex by the presence of several species reported to act as crop pathogens in plants as endophytes, without symptom development in the plant, and in the soil and plant residues as saprophytes. Taking into account the inoculum from stubble-borne pathogens and possible competition with other micro-organisms, it appears likely that the expression of a disease is the consequence of an imbalance between a potentially pathogenic species and the rest of the microbial community, rather than the consequence of the mere presence of this species [10].

Residues constitute a crucial ecological niche, not only for pathogenic species, but also for non-pathogenic and beneficial species. Residues can be viewed as both a fully-fledged matrix and a transient compartment, because they originate from the plant (temporal link), are

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in close contact with the soil (spatial link) and degrade over the following cropping season, at rates depending on the plant species, the cropping practices used [11], and the year (climate effect). It remains unknown whether the succession of microbial communities in residues is driven primarily by plant tissue degradation or edaphic factors [12]. Many studies have investigated the structure of the microbial communities present during the life cycle of the plant [e.g. 13–15], but few have investigated the microbiota associated with plant residues. Several ecological studies have investigated the impact of the residue compartment on the structure of soil microbial communities [2, 16–19], but not the impact of the soil compartment on structure of the residue communities. The detritusphere, defined as the part of the soil attached to residues [12, 20, 21], is the most extensive and broad hotspot of microbial life in the soil [22]. The residue compartment and the detritusphere are located in close physical proximity but are considered by microbiologists to be separate trophic and functional niches [23]. A description of the residue communities and the specific changes in these communities over time might, therefore, help agronomists to understand the impact of cropping practices on crop productivity. Fungi and bacteria play important roles in the degradation of plant tissues in debris (cellulose, hemicellulose, lignin), but the interactions between them within the microbial community remain unclear, due to the lack of information about their origins (air-borne, soil-borne or plant-borne), their individual functions and the drivers of community structure in residues.

Crop rotation induces changes in the composition of the soil microbial community and usually reduces pathogen pressure [e.g. 18]. For instance, wheat yields benefit from “break crops” such as oilseed rape or other non-host crops to break the life-cycle of wheat-specific pathogens [24]. We focused here on the wheat-oilseed rape rotation, one of the most widely used cropping systems in Europe. The areas under bread wheat and oilseed rape in France were 5.0×10^6 ha and 1.4×10^6 ha in 2017 [25], respectively. As oilseed rape usually recurs

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every three years in the rotation and is used almost systematically either directly before or directly after wheat, we estimate that this classical rotation is used on almost 4.2×10^6 ha every year. Half the area occupied by these two crops is now grown without tillage, with at least some of the residues of the preceding crop left on the soil [26]. The issue addressed here is thus directly relevant to more than 2×10^6 ha, or about one tenth of the total arable area in France.

In this study, we deliberately focused on crop residues as a neglected, transient, but fully-fledged half-plant/half-soil compartment without describing the soil microbial communities, considering that it has been already performed in several studies [e.g. 27, 28]. We tested the specific hypothesis that plant is a structuring factor of bacterial and fungal communities in residues, and that this effect decreases over time, as contact with the soil induce progressive colonization of residues by other microorganisms. Over the last few years, high-throughput metabarcoding has become an indispensable tool for studying the ecology of such complex microbial communities [29], partly due to the difficulties in isolating fungal and bacterial species and growing them in axenic conditions. We used this approach to describe and compare changes in the microbial community of wheat and oilseed-rape residues left on the soil surface of three cultivated fields during two cropping seasons. We investigated whether the three main determinants (plant species, cropping season, and rotation) of the diversity of fungal and bacterial communities affected the microbiota of crop residues.

Methods

Experimental design

Field plots and rotations – An extensive field experiment based on a wheat (W)-oilseed rape (O) rotation cropping system was carried out during the cropping seasons of 2015-2016 and 2016-2017 at the Grignon experimental station (Yvelines, France; 48°51’N, 1°58’E). This

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111 area is characterised by an oceanic climate (temperate, with no dry season and a warm
112 summer). A combined diachronic and synchronic strategy [30] was used to investigate the
113 dynamics of the residue microbial communities both over a two-year period on the same plot
114 and along a chronosequence substituting spatial differences (three plots) for time differences.
115 A first monoculture plot (WWW) was sown with the winter wheat cultivar Soissons. This plot
116 had been cropped with wheat since 2007 and was used in previous epidemiological studies
117 focusing on the impact of wheat debris on the development of Septoria tritici blotch [e.g. 31,
118 32, 33]. Two other plots were cropped with oilseed rape cv. Alpaga and wheat cv. Soissons in
119 rotation (OWO, adjacent to the WWW plot, and WOW, located 400 m away; Fig. 1). The
120 OWO and WWW plots are characterized by a silty clay loam soil, and plot WOW is
121 characterized by a silty loam soil (Additional file 1: Table S1). The three plots were not tilled
122 during the two cropping seasons. The wheat and oilseed rape residues were left on the soil
123 surface after harvest and partially buried to a depth of 10 cm with a disc harrow 6 weeks later
124 (late September). Crops were managed in a conventional way following local practices
125 (nitrogen fertilization, insecticide and herbicide treatments). No fungicide was sprayed on the
126 leaves during the study.

127 *Residue sampling* - Wheat and oilseed rape residues (150 samples) were collected over
128 the two cropping seasons. The changes in the microbial communities during residue
129 degradation were described on the basis of four sampling periods (October, December,
130 February, and May; Additional file 1: Table S2). A supplementary sample was taken in July
131 2016, and *a posteriori* in July 2017, to characterise the plant microbiota before the residues
132 came into contact with the soil. For each sampling period, twelve pieces of wheat residue or
133 four pieces of oilseed rape residue were collected from five points in each plot, 20 m apart
134 (Fig. 1).

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DNA extraction - Residues were cut to take off remaining roots, washed to remove the soil and air-dried in laboratory conditions. They were then cut into small pieces, pooled in a 50 mL bowl and crushed with a Retsch™ Mixer Mill MM 400 for 60 seconds at 30 Hz in liquid nitrogen, in a zirconium oxide blender. The crushed powder was stored in 50 mL Falcon tubes at -80°C until DNA extraction. We transferred 40 mg of crushed residues to a 2.0 mL Eppendorf tube, which was stored to -80°C. Total environmental DNA (eDNA) was extracted according to the TriZol® Reagent protocol (Invitrogen, according to the manufacturer's instructions). Two independent extractions were performed per sample, giving a total of 300 eDNA samples. The two extractions were considered to be technical replicates.

PCR and Illumina sequencing

Fungal and bacterial community profiles were estimated by amplifying ITS1 and the v4 region of the 16S rRNA gene, respectively. Amplifications were performed with the ITS1F/ITS2 [34] and 515f/806r [35] primers. All PCRs were run in a reaction volume of 50 µL, with 1x Qiagen Type-it Multiplex PCR Master Mix (Type-it® Microsatellite PCR kit Cat No./ID: 206243), 0.2 µM of each primer, 1x Q-solution® and 1 µL DNA (approximately 100 ng). The PCR mixture was heated at 95°C for 5 minutes and then subjected to 35 cycles of amplification [95°C (1 min), 60°C (1 min 30 s), 72°C (1 min)] and a final extension step at 72°C (10 min). PCR products were purified with Agencourt® AMPure® XP (Agencourt Bioscience Corp., Beverly, MA). A second round of amplification was performed with 5 µL of purified amplicons and primers containing the Illumina adapters and indexes. PCR mixtures were heated at 94°C for 1 min, and then subjected to 12 cycles of amplification [94°C (1 min), 55°C (1 min), 68°C (1 min)] and a final extension step at 68°C (10 min). PCR products were purified and quantified with Invitrogen QuantIT™ PicoGreen®. Purified amplicons were pooled in equimolar concentrations, and the final concentration of the library was

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160 determined with the qPCR NGS library quantification kit (Agilent). Libraries were sequenced
161 in five independent runs with MiSeq reagent kit v3 (600 cycles).
162
163 **Sequence processing**
164 Fastq files were processed with DADA2 v1.6.0 [36], using the parameters described in
165 the workflow for "Big Data: Paired-end" [37]. The only modification made relative to this
166 protocol was a change in the truncLen argument according to the quality of the sequencing
167 run. Taxonomic affiliations for amplicon sequence variants (ASV) generated with DADA2
168 were assigned with a naive Bayesian classifier on the RDP trainset 14 [38] and the UNITE 7.1
169 database [39].
170 Only ASV detected in both technical replicates were conserved for further analyses
171 [40], to ensure robustness. ASV classified as "Chloroplast", "Anthophyta", "Arthropoda",
172 "Cercozoa" or not classified at the phylum level were discarded from the datasets. The
173 remaining ASV were normalised according to the proportion of reads within each sample
174 [41].
175
176 **Microbial community analyses**
177 Microbial community profiles were obtained for 100 wheat residue samples and 50
178 oilseed rape residue samples. The diversity of each sample was estimated by calculating the
179 Shannon index with the ggpubr package in R [42]. A Kruskal-Wallis test was performed to
180 assess significant differences in residue diversity with time, between plants within a rotation
181 and between cropping seasons. In cases of significant differences, Wilcoxon pairwise tests
182 were performed to compare sampling periods. A Wilcoxon pairwise test was performed to
183 assess the effects of "plant" and "plant within a rotation" on Shannon index for each cropping
184 season. Divergences were considered significant if $p < 0.05$.

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"Plant" (i.e. crop), "crop within a rotation" and "cropping season" effects on community composition were assessed by multidimensional scaling (MDS) on the Bray-Curtis dissimilarity index with the phyloseq package in R (version 1.22.3 [43]). The effects of plant, cropping season, sampling period and biological sample on community composition were assessed with PERMANOVA, using the Adonis function of the vegan R package (version 2.4-4 [44]). After the aggregation of ASV for each sampling condition "sampling period/cropping year * crop within a rotation", the betapart R package [45] was used to determine whether temporal changes in community composition were due to turnover (i.e. replacement of ASV between two sampling periods) or nestedness (gain or loss of ASV between two sampling periods). The effect of the plant on the microbial communities associated with residues during degradation was also assessed with PERMANOVA on each sampling period, for each year.

The genus composition of fungal and bacterial communities was assessed with a cladogram based on genus names. Only genera observed in three biological samples harvested on the same plot were incorporated into the cladogram. A cladogram representing the number of ASV for each genus, read percentage, occurrence and distribution for each sample, was constructed with the Interactive Tree Of Live (iTOL [46]) online tool for phylogenetic trees.

To illustrate taxonomic changes over time, especially between plant-derived communities and communities involved later in the colonization of the residues, we focused on seasonal shifts (increase, decrease or stability) in the relative abundance of a selection of some fungal and bacterial genera and tested their statistical significance (Wilcoxon tests between sampling periods).

Results

The bacterial and fungal communities associated with wheat (W) and oilseed rape (O) crop residues were characterised on three plots: a wheat monoculture (WWW), and two oilseed

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rape-wheat rotation plots (WOW and OWO) (Fig. 1). We assessed the composition of these microbial communities four times per year, during two consecutive cropping seasons (in October, December, February and May). An additional time point (in July) was also included for identification of the micro-organisms present on the plant before contact with the soil (Additional file 1: Table S2). An analysis of raw sequence datasets for the 150 samples of wheat and oilseed rape residues collected over the two cropping seasons resulted in the grouping of 14,287,970 bacterial and 9,898,487 fungal reads into 2,726 bacterial and 1,189 fungal amplicon sequence variants (ASV). ASV not detected in both technical replicates (5.4% of bacterial reads and 1.5% of fungal reads; Additional file 1: Table S3) were removed from the datasets.

Alpha diversity

Fungal and bacterial diversity was influenced by cropping season – Diversity dynamics, assessed by calculating the Shannon index, differed between the two cropping seasons and between fungi and bacteria. It was influenced only slightly by the type (or the absence) of rotation (Fig. 2). Fungal diversity increased over time during the first cropping season, whereas the differences between the samples in the second year did not reflect a gradual increase. Bacterial diversity did not increase during the first cropping season, except for wheat residues in rotation (WOW). During the second year, diversity increased from December to May, for all conditions. The impact of climatic conditions during residue degradation (Additional file 1: Table S4) or differences in initial diversity on the plant before harvest may explain the less marked trends observed between the two cropping seasons.

Fungal and bacterial diversity are influenced by plant species and rotation – Oilseed rape residues supported less fungal diversity than wheat residues in 2015-2016, but not in 2016-2017 (Additional file 1: Table S6). The opposite trend was observed for bacteria:

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bacterial diversity in oilseed rape was significantly lower than that in wheat in 2016-2017, but there was no difference in bacterial diversity between the two crops in 2015-2016. In addition, the Shannon index was significantly higher in wheat grown in monoculture than in wheat grown in rotation for both years for fungi and in 2015-2016 for bacteria.

Comparison of microbial communities associated with residues

We analysed the effects of plant species, rotation, cropping season and sampling period on communities, using the Bray-Curtis index and PERMANOVA. Differences between sample replicates collected from the same plot during the same sampling period were not significant for bacterial or fungal communities (Table 1). Thus, there was remarkably little heterogeneity between the samples from the same plot, and the number of biological samples was, therefore, sufficient to assess differences due to the variables of interest (i.e. plant species, rotation, cropping season and sampling period).

The structure of bacterial and fungal communities is influenced by plant species and rotation – Oilseed rape and wheat residues presented different sets of ASV, for both bacterial and fungal communities (Fig. 3). Plant species was the main factor explaining differences between the communities, accounting for 22.7% of the variance for bacteria and 32.4% for fungi (Table 1). The effect of plant species on fungal community structure decreased over time, while the effect of plant species on bacterial community structure tended to increase between October and December (Additional file S1: Table S5). For wheat, the type of rotation (i.e. rotation or monoculture) accounted for 10.5% of the variance for fungal community composition and 6.6% of the variance for bacterial community composition (Table 1).

Community structures change over time – Cropping season was the main temporal factor underlying changes in community structure, accounting for 16.4% of the variance for bacteria and 12.5% of the variance for fungi (Table 1). Sampling period also had a significant

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impact on community composition, accounting for 17.2% of the variance for bacteria and 7.2% of the variance for fungi. Theoretically, changes in ASV composition result from turnover (replacement of ASV between two sampling periods) and nestedness (gain or loss of ASV between two sampling periods [45]). We found that the dissimilarity between sampling periods was smaller for bacterial than for fungal ASV structure. By breaking down the dissimilarity between sampling periods, we found that most of the changes in fungal and bacterial ASV structure were due to turnover (Additional file 1: Table S7). Furthermore, we found that nestedness had a greater impact on bacterial communities than on fungal communities.

Changes in communities, by genus

Community succession across the different sampling dates was explained largely by the turnover of ASV. We characterised potential taxonomic differences in communities over time by analysing wheat and oilseed rape residues separately. ASV were aggregated together at genus level, resulting in 84 fungal (Fig. 4) and 184 bacterial genera (Additional file 1: Fig. S1, S2) for wheat, and 63 fungal (Fig. 5) and 186 bacterial genera (Additional file 1: Fig. S3, S4) for oilseed rape. For both plant species, we identified genera that disappeared or displayed a significant decrease in relative abundance over time (Additional file: Fig. S5). Among these genera, some are known to be associated with plants, such as *Alternaria*, *Acremomium* [14, 47, 48], *Cryptococcus* [49], *Sarocladium* [50] and *Cladosporium* [13, 47–50].

Some of the fungal species detected on wheat, such as *Oculimacula yallundae* (all ASV of *Oculimacula* genera), *Zymoseptoria tritici* and *Pyrenophora tritici-repentis,* are known to be pathogenic. Some of the species detected on oilseed rape, such as *Verticillium* spp., *Leptosphaeria maculans* (= *Plenodomus maculans*) and *Leptosphaeria biglobosa* (= *Plenodomus biglobosa*), are also known to be pathogenic. Strikingly, *L. maculans* and *L.*

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285 *biglobosa* predominated over the other taxa. *Verticillium longisporum*, *V. dahlia* and *V. albo-*
286 *atrum* were mostly detected during the second sampling year. As samples were collected in
287 two different fields, it was not possible to determine whether the occurrence of *Verticillium*
288 spp., a soil-borne pathogen complex causing *Verticillium* wilt [51], was affected more by year
289 or by the soil contamination. *Acremomium*, *Clonostachys* and *Alternaria* genera, which have
290 also been described as associated with plants [52], were detected in the early sampling periods
291 (Additional file: Fig. S5). Their relative abundances decreased over time. Most of the genera
292 that were not present at early sampling points and with relative abundances increasing over
293 time (e.g. *Coprinellus*, *Psathyrella*, *Torula*, *Tetracladium*, and *Exophiala*) were common to
294 wheat and oilseed rape residues. These genera can thus be considered as probably derived
295 primarily from the surrounding soil.

296 For bacteria, the difference in the genera detected between the two plants species was
297 less marked than for fungi, as 146 genera were common to wheat and oilseed rape residues.
298 These 146 genera corresponded to the 98.7% most prevalent reads for wheat and 97.5% most
299 prevalent genus reads for oilseed rape. *Proteobacteria* was the predominant phylum the first
300 year. The most prevalent proteobacterial subgroup was *Alphaproteobacteria*, with a high
301 prevalence of *Rhizobiales* and *Sphingomonadales*. *Rhizobium* and *Neorhizobium*, two major
302 genera from *Rhizobiales*, decreased in abundance between October and May in both wheat
303 and oilseed rape. *Sphingomonadales* genera were much more abundant on wheat than on
304 oilseed rape, especially *Sphingomonas*. *Bacteroidetes* genera, including *Pedobacter* in
305 particular, were frequently detected and their prevalences tended to be stable for oilseed rape
306 residues, and to decrease for wheat residues. In parallel, an increase in *Actinobacteria*,
307 particularly *Nocarioides*, was observed. Major differences between July and October were
308 observed for oilseed rape, consistent with the beta-diversity analysis, in which the percentage
309 dissimilarity between July and October was high, due to both species extinction and turnover.

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Gammaproteobacteria were highly abundant on oilseed rape in July. Their frequency then decreased rapidly from October to May, due largely to the decrease in *Pseudomonas*. In parallel, we observed an increase in the levels of *Alphaproteobacteria*, especially *Rhizobium* and *Sphingomonas*, between July and October. A small decrease in levels of *Gammaproteobacteria* was observed between July and October for wheat in rotation, whereas the percentage of reads associated with this class increased between July and December for wheat in monoculture, due largely to the decrease in *Pantoea* and *Enterobacteria*. The abundance of *Bacteroidetes*, especially *Pedobacter* and *Flavobacterium*, also increased between July and October.

Discussion

Most studies on crop residues have focused on their impact on soil microbial communities [16], and the rare studies investigating the impact of soil on residue communities focused exclusively on bacteria [27, 28] or fungi [53]. Most of these studies were conducted on residues from a single year. Bastian et al. [12] established an extensive description of the species present in the soil, detritusphere and wheat residues, using sterilised residues and soil in a microcosm. In this study, we showed, under natural conditions, that three main factors (plant species, cropping season, rotation) simultaneously influence the composition of both fungal and bacterial communities present on residues. This study is the first to investigate the total fungal and bacterial communities associated with wheat and oilseed rape residues by a metabarcoding approach over two consecutive years. The very low variability of the communities for the five replicates is remarkable and shows that our strategy would be appropriate for comparing the effects of different treatments on microbial communities.

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Crop residues should be viewed as a shifting platform for microbial meeting strongly affected by plant species

Oilseed rape and wheat residues contained different sets of micro-organisms before soil contact and during the firsts sampling dates after harvest. Similar results were previously obtained for the bacterial communities of buried crop residues [28]. Consistent with the findings of this previous study, the divergence between wheat and oilseed rape bacterial communities was probably due to differences in the chemical compounds present in the plants. The rapid change in the community observed at early stages of residue degradation for oilseed rape may be explained by the modification of simple compounds (sugars, starch, etc.), whereas wheat is composed of more complex compounds (lignin) and is, therefore, broken down less quickly, resulting in a slower change in the microbial community [28]. Overall, the change in bacterial community composition highlights turnover between copiotrophs and oligotrophs. Although copiotrophy and oligotrophy are physiological traits, several attempts have been made to classify microorganisms as oligotrophs and copiotrophs based on phylogeny [54]. According to this generalization, bacterial and fungal taxa whose relative abundances are significantly decreased during succession belong mainly to copiotroph. These taxa include for instance *Alternaria*, *Cladosporium*, *Massilia* and *Pseudomonas* (Additional file: Fig. S5). In contrast, the relative abundances of oligotrophic taxa such as *Coprinellus* or *Nocardiodes* increased during residues degradation, which could be indicative of the superior abilities of these micro-organisms to degrade complex polymers.

The initial fungal communities were structured mostly by the presence of species originating from the plant, several of which were highly specialised on the host plant. These species were gradually replaced by more generalist species, which colonised the residues of both plants. Most of these generalists, such as *Exophiala*, *Coprinellus* and *Torula*, are known to be soil-born [55, 56], or involved in degradation, such as *Coprionopsis* [57]. The host-

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359 specific fungi identified in our study included a large number of ascomycetes known to be
360 foliar pathogens (*O. yallundae*, *Fusarium* sp. and *Gibberella* sp., *Z. tritici*, *P. tritici-repentis*,
361 *Parastagonospora nodorum*, *Monographella nivalis*, *L. biglobosa* and *L. maculans*). The
362 lifestyles of some pathogens are well-documented, as for *Z. tritici*, *P. tritici-repentis* and *L.*
363 *maculans*. The decrease with time in levels of *Z. tritici* and other pathogens in wheat residues
364 contrasts with the persistence of *L. maculans* and *L. biglobosa* in oilseed rape residues. These
365 three pathogens are all known to reproduce sexually on the residues of their host plant [31,
366 58], but the life cycle of *L. maculans* is characterised by systemic host colonisation through
367 intracellular growth in xylem vessels [59], whereas the development of *Z. tritici* is localised
368 and exclusively extracellular [60]. Oilseed rape residues thus provide *L. maculans* with
369 greater protection than is provided to *Z. tritici* by wheat residues. This likely explains
370 differences in the persistence of the two pathogens and in the temporal dynamics of ascospore
371 release: over up to two years for *L. maculans* [61, 62] but only a few months for *Z. tritici* [31,
372 63]. The predominance of *L. maculans* on oilseed rape residues was not surprising given that
373 the oilseed rape cultivar Alpaga is known to be susceptible to *L. maculans*, but the high
374 abundance of *L. biglobosa* was much more remarkable. One surprising finding of our study
375 was the constant association of *L. maculans* with *L. biglobosa* on residues. Indeed, *L.*
376 *biglobosa* is known to be more associated with upper-stem lesions [64], and its presence in
377 large amounts on residues has never before been reported.

378 Our findings are consistent with current epidemiological knowledge of emblematic
379 wheat and oilseed rape diseases, but they highlight our lack of knowledge concerning the
380 lifestyles of many other fungal pathogens present on residues. A key point to be taken into
381 account is that the trophic status of many species known to be principally pathogenic or non-
382 pathogenic is not definitive [65]. For instance, *Alternaria infectoria* is sometimes described as
383 a pathogen of wheat [13, 66], sometimes as an endophyte [67], and has even been tested as a

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potential biocontrol agent against *Fusarium pseudograminearum* on wheat [68]. Crop residues, half-plant/half-soil, should be the focus of future studies aiming to disentangle the succession of microbial species with different lifestyles and to characterise their relative impacts on the development of currently minor, but potentially threatening diseases.

The residue microbiota should be analysed in a dynamic manner, both within and between years

The results of our study highlight the importance of conducting multi-year studies focusing on ecological dynamics both within and between years in natural conditions. Year had a strong effect on both bacterial and fungal communities. Fluctuations of climatic conditions (temperature, rainfall, wind) have a major impact on pathogenesis (disease triangle concept [69]) and on the saprophytic survival of plant pathogens during interepidemic periods [70]. The two years of our study were marked by similar means of 10-day mean temperatures, but large differences in rainfall: mean 10-day cumulative rainfall in the first year was almost twice that in the second (Additional file 1: Table S7). The colonisation of residues by late colonisers may be affected by such climatic differences: in wheat, most prevalent degrading fungi (like *Coprinellus*, *Psathyrella*, *Coprinopsis*) were almost absent in the second year of the study. There was also considerable dissimilarity between the bacterial communities associated with each of the two years. For example, genus *Enterobacter*, which was highly abundant in the second year, was barely detectable in the first year.

Crop rotation has little impact on residue microbial communities

Oilseed rape is never grown in monoculture, so the effect of crop rotation was assessed only for wheat. The effect of rotation on residue microbial communities was much smaller than the effect of year (cropping season). It was more marked for fungi, for which diversity

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409 was greater in monoculture than in rotation. The use of a rotation may prevent the most
410 strongly specialised species, in this case fungi, from becoming established, regardless of their
411 pathogenicity. This finding is consistent with the greater development of some diseases in
412 monoculture conditions, which promote the maintenance of pathogens through the local
413 presence of primary inoculum. For instance, the presence of *P. tritici-repentis*, agent of tan
414 spot disease, in the wheat monoculture plot and its absence from wheat-oilseed rape plots is
415 consistent with epidemiological knowledge indicating that this disease can be controlled by
416 leaving a sufficient interval between consecutive wheat crops in the same field [71].
417
418 **Lesson to be learned from the residue microbial communities for the sustainable**
419 **management of debris-borne diseases: a delicate balance between pathogenic and**
420 **beneficial micro-organisms**
421 The maintenance of crop residues at the surface of the cultivated soil increases the
422 microbial diversity of the soil and, in some ways, helps to maintain good functional
423 homeostasis [72]. However, conservation practices tend to increase the risk of foliar diseases
424 [4–6]. Most disease management strategies focus on epidemic periods, during which the
425 pathogen and its host are in direct contact. Interepidemic periods are also crucial for pathogen
426 development, although during these periods the primary inoculum is not directly in contact
427 with the new crop whilst not present in the field. Indeed, by carrying the sexual reproduction
428 of several fungal pathogens, residues contribute to the generation and transmission of new
429 virulent isolates potentially overcoming resistance genes, during monocyclic epidemics, as
430 described for oilseed rape canker caused by *L. maculans* [73], but also polycyclic epidemics,
431 as described for Septoria tritici blotch caused by *Z. tritici* [74].
432 However, the results of our study suggest that residues should not only be considered as
433 a substrate for pathogens and a potential source of inoculum. Indeed, we detected several

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434 fungi identified as beneficial or even biocontrol agents in previous studies, such as
435 *Clonostachys rosea*, *Aureobasidium pullulans*, *Chaetomium globosum* and *Cryptococcus* spp..
436 *C. rosea*, which was detected in both oilseed rape and wheat residues, has been reported to
437 limit the sexual and asexual reproduction of *Didymella rabiei* on chickpea residues by
438 mycoparasitism [75]. It has also been reported to be effective against *Fusarium culmorum* on
439 wheat plants, through antibiosis during the epidemic period [76], and on wheat residues,
440 through antagonism during the interepidemic period [77]. *Cladosporium* spp., which were
441 abundant in our study, have also been reported to inhibit the development of *P. tritici-repentis*
442 on wheat plants [78] and of *Fusarium* spp. on wheat residues [77]. The presence of these
443 fungal species on wheat and oilseed rape residues is of potential interest for future analyses of
444 interactions. Due to the use of a low-resolution marker for bacterial characterisation, we were
445 unable to identify similarly the bacteria potentially interacting with pathogenic fungi. For
446 instance, the presence of *Pseudomonas* spp. suggests possible interactions both with other
447 microbial species and with the host plant [79], but the nature of the potential interactions is
448 indeterminate: species of the *Pseudomonas fluorescens* group are known to be beneficial to
449 plants, whereas *Pseudomonas syringae* and *Pseudomonas aeruginosa* are known to be
450 pathogens of plants and even humans.

451 Although our study reveals the presence of genera or species reported in the literature as
452 biocontrol agents, it has not yet shown any interaction between them and the pathogens. This
453 experimental study (sampling effort, residue treatments, etc.) was not designed to characterize
454 such interactions. A strategy involving the inference of microbial interaction networks from
455 metabarcoding datasets might help to identify the species beneficial against pathogens,
456 through competition, antagonism or parasitism. This however requires a more analytical,
457 comparative experimental approach, that goes beyond the only description of shifts in natural
458 communities composition: for example, using different “treatments” in a broad sense (e.g.

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459 artificial inoculation with a species or a group of species, change of biotic or abiotic
460 environmental conditions, etc.) in order to modify interaction networks and so highlight the
461 impact of some groups of micro-organisms on the whole community or a given species.
462

463 ## Conclusion

464 This study shows that crop residues, which can be seen as half-plant/half-soil transient
465 compartment, constitute a pivotal fully-fledged microbial ecosystem that has received much
466 less attention than the phyllosphere and rhizosphere to date. This study therefore fills a gap in
467 knowledge of the communities present on crop residues under natural conditions. It confirms
468 that the microbiote of crop residues should be taken into account in the management of
469 residue-borne diseases. Taking into account this ecosystem is essential, not only to improve
470 the quantitative management of crop residues, but also to identify groups of beneficial micro-
471 organisms naturally present. The beneficial elements of the microbial community should be
472 preserved, or even selected, characterised and used as biological control agents against the
473 pathogens that complete their life cycle on the residues. These results are particularly
474 important in that wheat-oilseed rape rotations are among the most widespread arable cropping
475 systems in France and Europe.
476

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Availability of data and materials

The raw sequencing data is available from the European Nucleotide Archive (ENA) under the study accession PRJEB27255 (Sample SAMEA4723701 to SAMEA4724326). We provide the command-line script for data analysis and all necessary input files as Additional File 2.

Authors' contributions

LK, FS, VL, MHB, MB conceived the study, participated in its design, and wrote the manuscript. LK conducted the experiments and analysed the data. FS and VL supervised the project. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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Tables

Table 1 - Results of the PERMANOVA test analysing the effects of plant, rotation, cropping season, and sampling period on the fungal and bacterial communities present in oilseed rape and wheat residues

		Fungi		Bacteria	
Data set	Factors	R^2	*p*-value	R^2	*p*-value
Overall	Plant [1]	0.324	<0.001	0.227	<0.001
	Replicate [2]	0.016	1	0.011	1
	Cropping season	0.125	<0.001	0.164	<0.001
	Sampling period	0.072	0.002	0.172	<0.001
2015-2016 samples	Plant [1]	0.422	<0.001	0.368	<0.001
	Sampling period	0.099	0.021	0.186	<0.001
2016-2017 samples	Plant [1]	0.418	<0.001	0.300	<0.001
	Sampling period	0.118	0.009	0.241	<0.001
July 2017 samples	Plant [1]	0.755	0.004	0.696	<0.001
Wheat samples	Crop within a rotation	0.105	<0.001	0.066	<0.001
	Cropping season	0.334	<0.001	0.328	<0.001

[1] comparison between oilseed rape and wheat, regardless of the rotation.

[2] five sampling points per plot.

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Figures

Figure 1 - Experimental layout of the experiment. **(A)** Plots (WWW, WOW and OWO) used during the two years of the experiment at the INRA Grignon experimental station (Yvelines, France). WWW: plot cropped with winter wheat since 2007. WOW and OWO: plots cropped with a wheat-oilseed rape rotation since 2014. Wheat straw and oilseed rape debris were chopped at harvest and left on the soil surface. The dashed line indicates the sampling transect. **(B)** Oilseed rape residues in a plot cropped with wheat (OWO or WOW). **(C)** Wheat residues in a plot cropped with oilseed rape (WOW or OWO). (D) Wheat residues in the wheat monoculture crop (WWW).

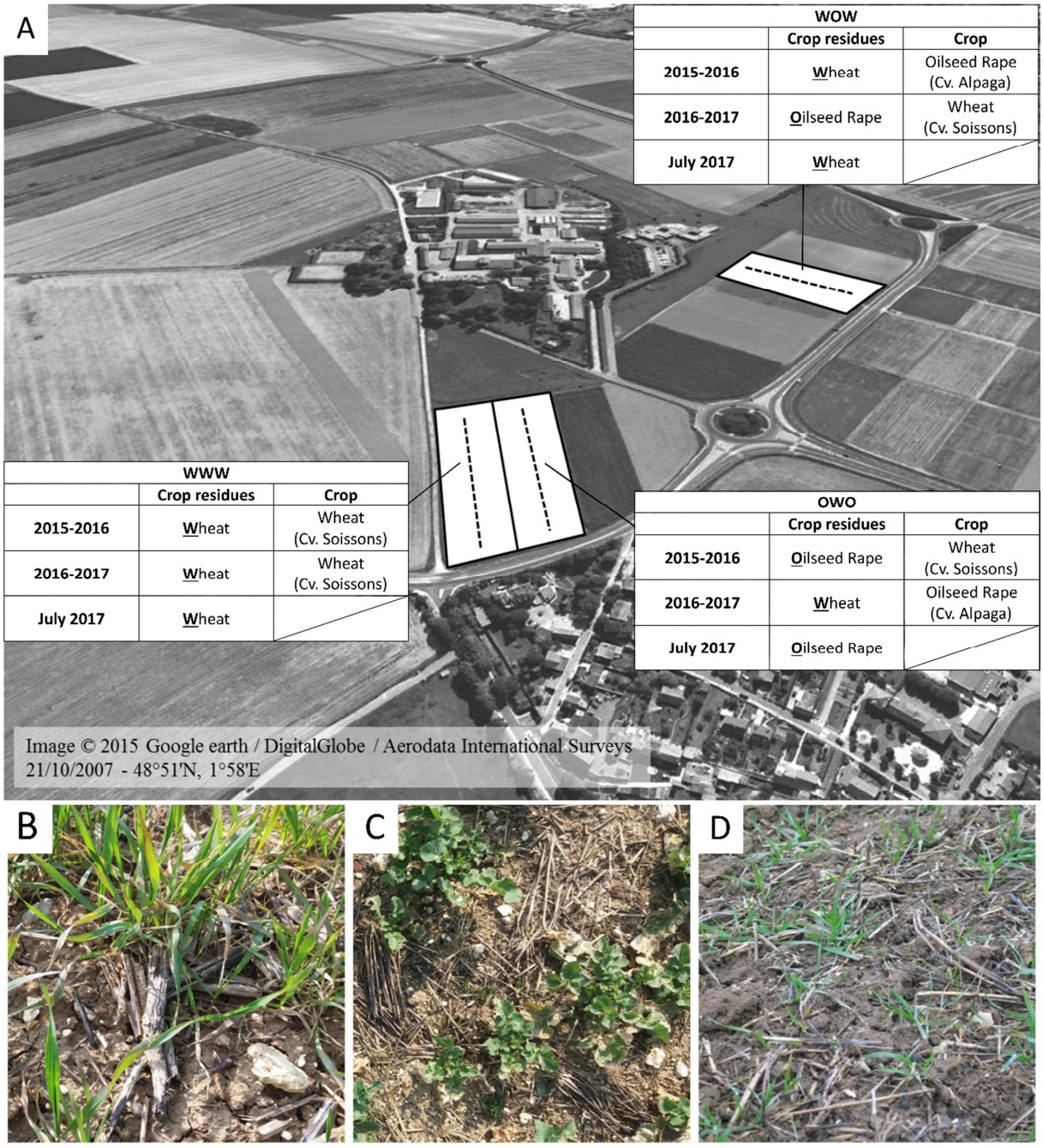

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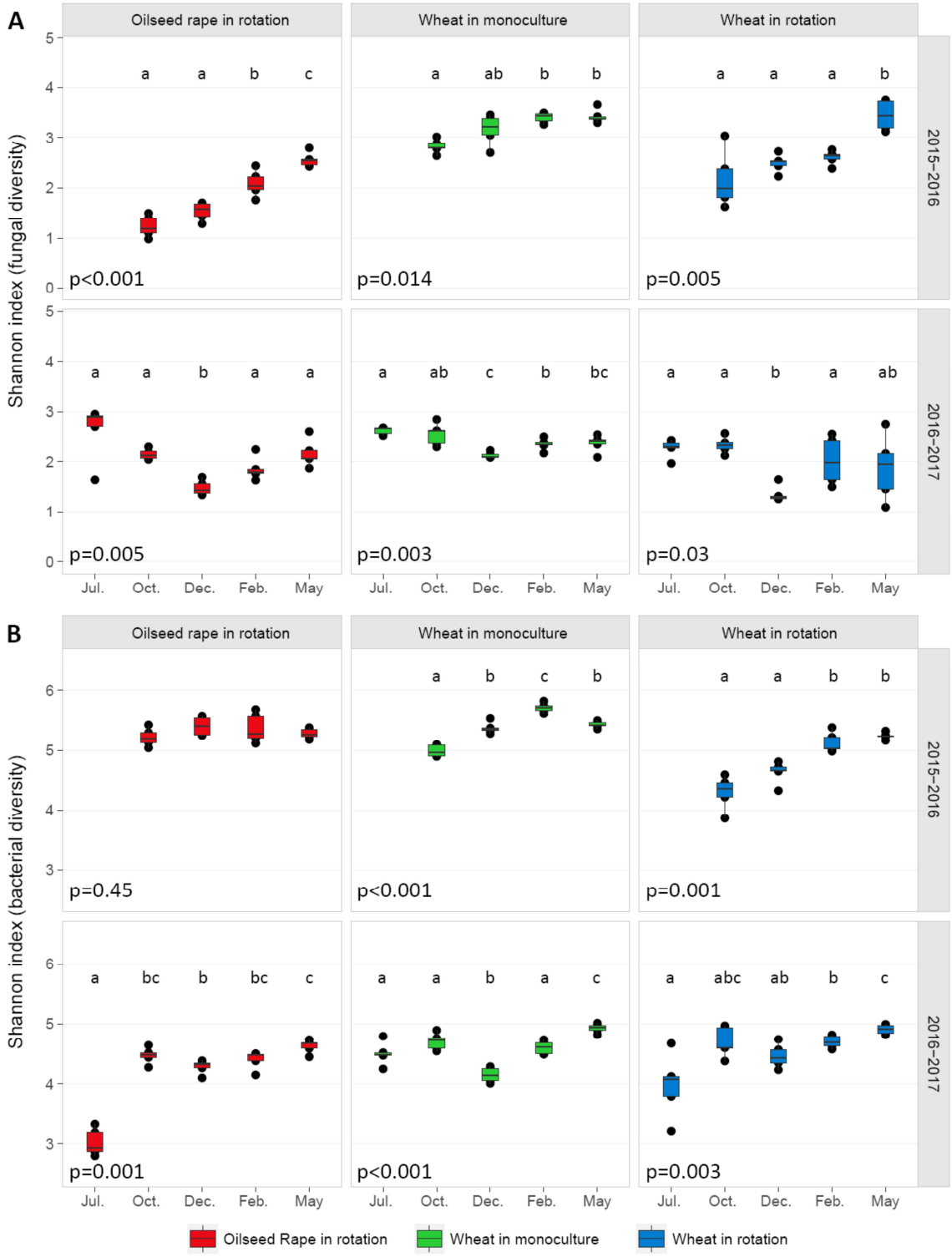
Figure 2 - Fungal (**A**) and bacterial (**B**) diversity in plants (July) and residues (October, December, February, May), as assessed with the Shannon index, according to sampling period, the crop within a rotation (oilseed rape in OWO or WOW, wheat in WWW, wheat in WOW or OWO) and the cropping season (2015-2016, 2016-2017). Each box represents the distribution of Shannon index for five sampling points. Kruskal-Wallis tests were performed for each "crop within a rotation * cropping season" combination (*p*-values are given under each graph). Wilcoxon tests between sampling periods were performed when the Kruskal-Wallis test revealed significant differences. Samples not sharing letters are significantly different.



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762 **Figure 3** - Structure of the fungal (**A**) and bacterial (**B**) communities present in oilseed rape
763 and wheat residues, according to compositional dissimilarity (Bray-Curtis distance), after
764 multidimensional scaling (MDS). The two MDS were performed on the overall dataset and
765 faceted according to the sampling period. Each point represents one sample corresponding to
766 a cropping season (shape: 2015-2016; 2016-2017; 2017-2018) and crop within a rotation
767 (colour: oilseed rape in rotation, i.e. in WOW and OWO; wheat monoculture, i.e. in WWW;
768 wheat in rotation, i.e. in WOW and OWO).

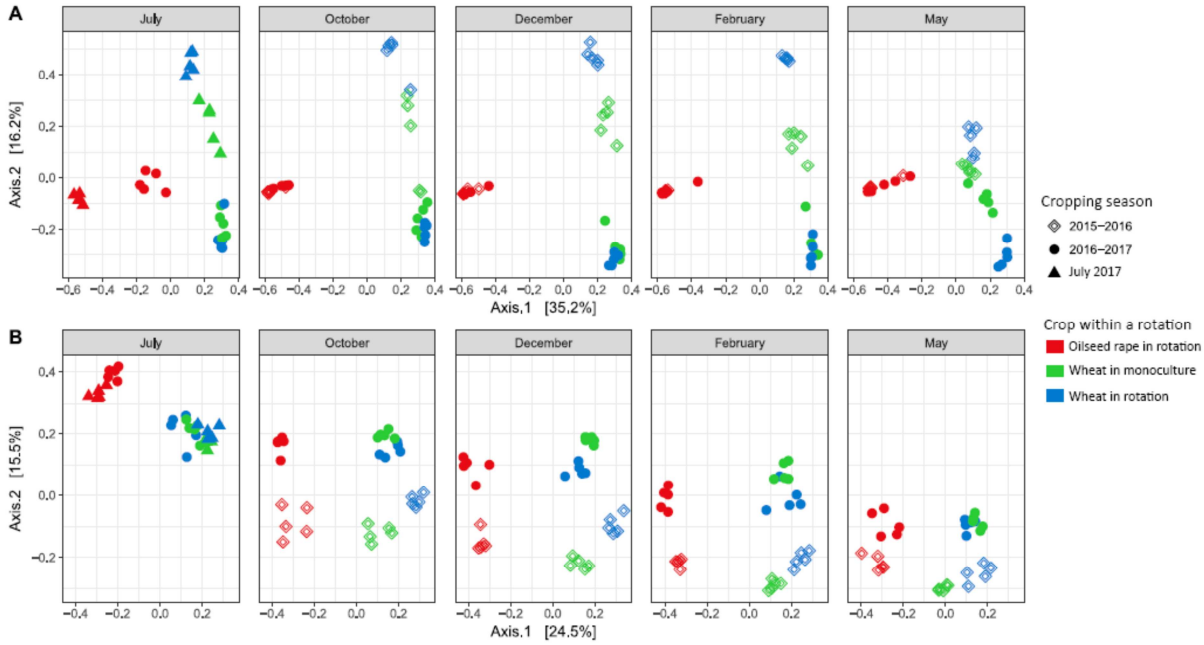

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Figure 4 - Distribution of the most prevalent fungal genera detected in wheat residues. (**A**) Cladogram of the most prevalent genera. Genera were filtered according to their occurrence (at least three times in the five sampling points for each "crop within a rotation * cropping season * sampling period" combination). Unclassified genera were removed from the tree. (**B**) Number of ASV of each genus. (**C**) Occurrence of each ASV in the 100 samples of wheat residues. (**D**) Percentage of reads for each genus. (**E**) Distribution of each genus in the five samples per date (increasing number of reads shown on a scale running from yellow to red).

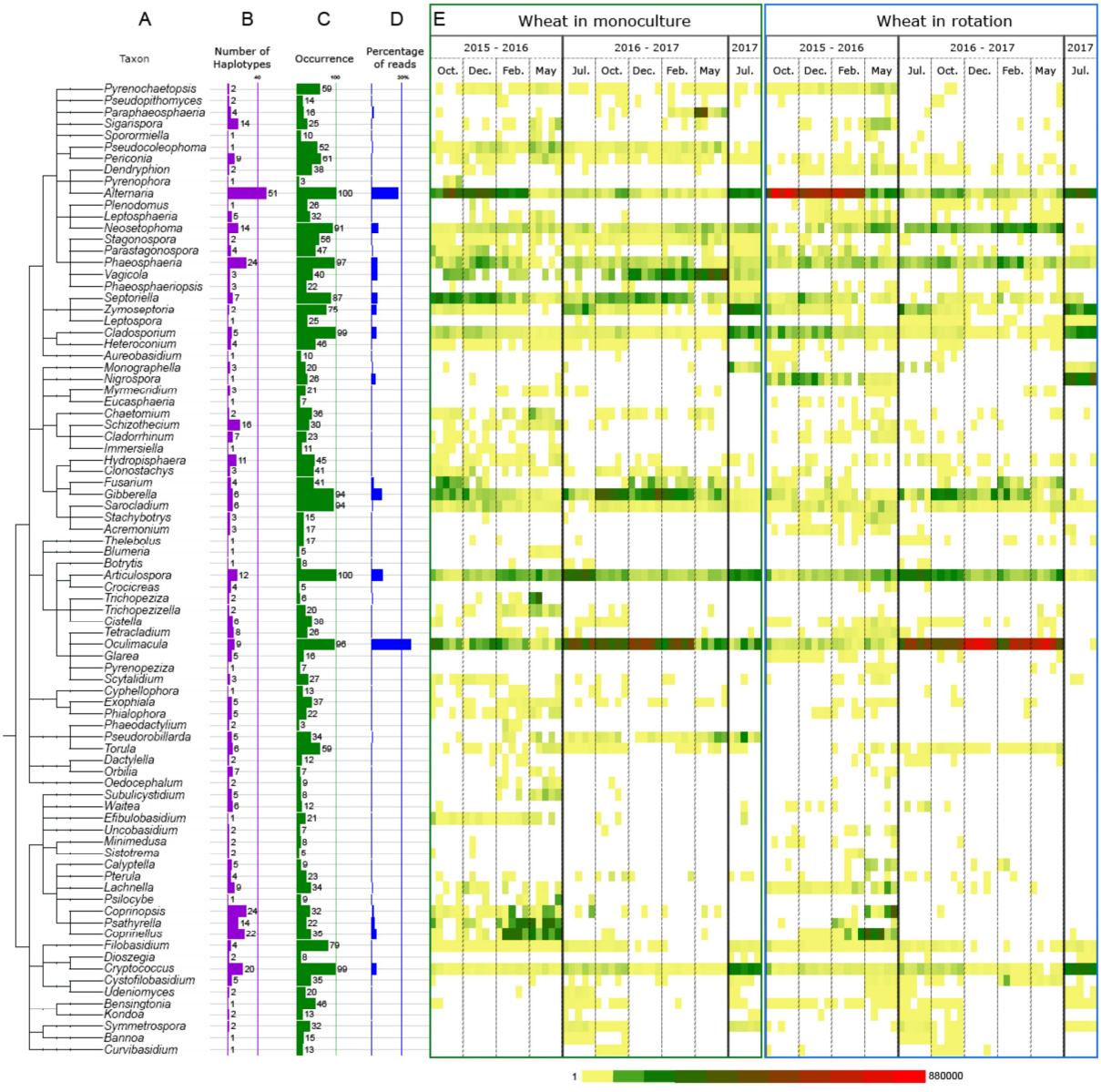

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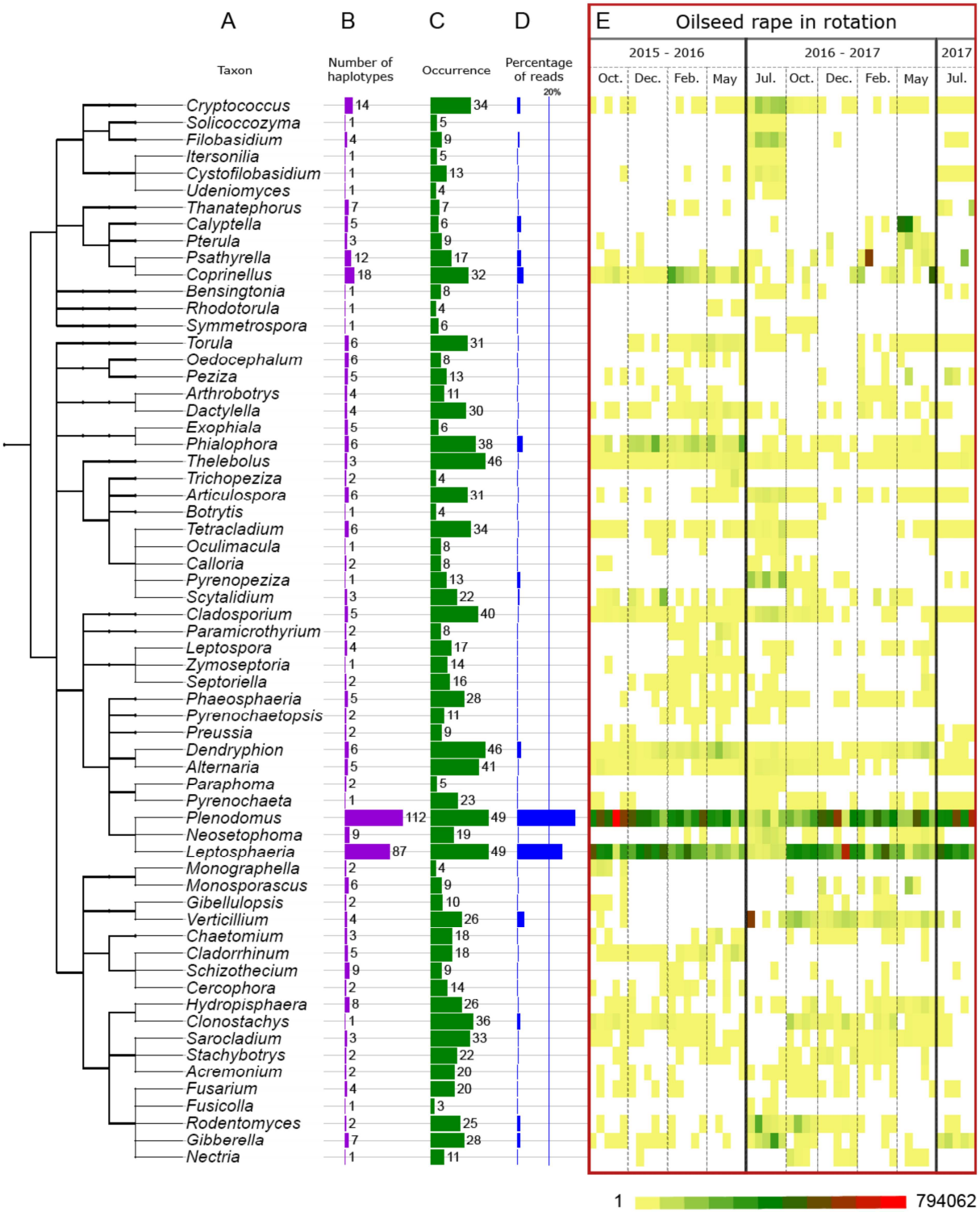
Figure 5 - Distribution of the most prevalent fungal genera detected in oilseed rape residues. (**A**) Cladogram of the most prevalent genera. Genera were filtered according to their occurrence (at least three times in the five sampling points for each "crop within a rotation * cropping season * sampling period") combination. Unclassified genera were removed from the tree. (**B**) Number of ASV for each genus. (**C**) Occurrence of each ASV in the 50 samples of oilseed rape residues. (**D**) Percentage of reads for each genus. (**E**) Distribution of each genus in the five samples per date (increasing number of reads shown on a scale from yellow to red).



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Additional files

Table S1 - Soil texture of the three plots (WWW, OWO and WOW).

	WWW, OWO	WOW
Clay (%)	27.4	18.2
Silt (%)	53.2	61.2
Sand (%)	18.8	20.4

Table S2 - Sampling dates of wheat and oilseed rape plants (July) and residues (October, December, February and May) for each cropping season.

Cropping season	July	October	December	February	May
2015-2016	/	23.10.2015	04.12.2015	26.02.2016	19.05.2016
2016-2017	11.07.2016	17.10.2016	05.12.2016	06.02.2016	15.05.2017
2017-2018	07.07.2017	/	/	/	/

Table S3 - Total number of reads and percentage (in brackets) remaining after ASV filtering.

	After DADA2	After replicate suppression	After taxon suppression
Bacterial reads	14,287,970	13,509,461 (94.6%)	13,228,976 (92.6%)
Fungal reads	9,898,487	9,753,628 (98.5%)	9,628,995 (97.3%)
Bacterial haplotypes	19,235	2,905	2,726
Fungal haplotypes	3,587	1,241	1,189

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Table S4 - *P*-values from Wilcoxon pairwise test comparisons for bacterial and fungal diversity. The *p*-values were calculated from the Shannon index between crops within a rotation (wheat in monoculture, i.e. in WWW; wheat in rotation, i.e. in WOW or OWO; oilseed rape in rotation, i.e. in OWO or WOW) or between crops whatever the rotation (wheat; oilseed rape) for each year. Pairwise tests were performed for all sampling periods in each cropping season (20 samples for each crop within a rotation in 2015- 2016; 25 in 2016-2017; 5 in July 2017). Significant *p*-values are underlined.

	Pairwise comparisons	2015-2016	2016-2017	July 2017
Bacterial diversity	Wheat (monoculture) – Wheat (rotation)	<u>≤0.001</u>	0.801	<u>0.012</u>
	Wheat (rotation) – Oilseed rape	<u>≤0.001</u>	<u>0.004</u>	<u>0.037</u>
	Wheat (monoculture) – Oilseed rape	0.297	<u>0.004</u>	<u>0.037</u>
	Wheat – Oilseed rape	0.1	<u>≤0.001</u>	1
Fungal diversity	Wheat (monoculture) – Wheat (rotation)	<u>0.001</u>	<u>0.0018</u>	<u>0.012</u>
	Wheat (rotation) – Oilseed rape	<u>≤0.001</u>	0.849	<u>0.012</u>
	Wheat (monoculture) – Oilseed rape	<u>≤0.001</u>	<u>0.002</u>	<u>0.012</u>
	Wheat – Oilseed Rape	<u>≤0.001</u>	0.095	<u>0.03</u>

Table S5 - Summary of meteorological data (temperature, rainfall) for the INRA Grignon experimental station (Yvelines, France), obtained from the CLIMATIK INRA database (https://intranet.inra.fr/climatik_v2/) from July 1st to May 31st of the following year, for the cropping seasons 2015-2016 and 2016-2017.

	10-day mean temperature (°C)		10-day cumulative rainfall (mm)	
	2015-2016	2016-2017	2015-2016	2016-2017
Mean	11.2	10.8	22.6	12.3
Minimum	2.0	0.9	0	0
Maximum	21.8	21.4	131	55

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Table S6 - Plant effect (wheat vs. oilseed rape) on community dispersion. This effect was tested by applying the Adonis function of the vegan R package to the Bray-Curtis dissimilarity index. *P*-values (not shown) were all < 0.02.

	Fungi				Bacteria			
	All	2015-2016	2016-2017	2017	All	2015-2016	2016-2017	2017
July	0.372	/	0.611	0.755	0.423	/	0.540	0.696
October	0.495	0.612	0.755	/	0.367	0.520	0.659	/
December	0.486	0.688	0.691	/	0.370	0.573	0.641	/
February	0.429	0.541	0.651	/	0.409	0.643	0.611	/
May	0.273	0.337	0.401	/	0.315	0.435	0.508	/

Table S7 - Decomposition of dissimilarity due to temporal changes in fungal (F) and bacterial (B) community composition. Total dissimilarity is broken down into turnover (replacement of ASV) and nestedness (gain or loss of ASV).

Crop within a rotation	Season	Sampling period compared	Total dissimilarity		Turnover		Nestedness	
			F	B	F	B	F	B
Oilseed rape	2015-2016	Oct. - Dec.	0.622	0.318	0.618	0.219	0.005	0.099
Oilseed rape	2015-2016	Dec. - Feb.	0.650	0.321	0.577	0.290	0.073	0.031
Oilseed rape	2015-2016	Feb. - May	0.591	0.390	0.565	0.202	0.027	0.188
Oilseed rape	2016-2017	Jul. - Oct.	0.652	0.554	0.648	0.250	0.004	0.304
Oilseed rape	2016-2017	Oct. - Dec.	0.620	0.353	0.549	0.217	0.071	0.136
Oilseed rape	2016-2017	Dec. - Feb.	0.585	0.353	0.516	0.276	0.068	0.077
Oilseed rape	2016-2017	Feb. - May	0.529	0.384	0.529	0.342	0.000	0.042
Wheat in monoculture	2015-2016	Oct. - Dec.	0.427	0.330	0.425	0.142	0.002	0.188
Wheat in monoculture	2015-2016	Dec. - Feb.	0.444	0.294	0.416	0.190	0.028	0.104
Wheat in monoculture	2015-2016	Feb. - May	0.444	0.458	0.424	0.255	0.020	0.203
Wheat in monoculture	2016-2017	Jul. - Oct.	0.438	0.346	0.424	0.300	0.014	0.046
Wheat in monoculture	2016-2017	Oct. - Dec.	0.463	0.330	0.257	0.113	0.207	0.217
Wheat in monoculture	2016-2017	Dec. - Feb.	0.386	0.248	0.311	0.200	0.075	0.048
Wheat in monoculture	2016-2017	Feb. - May	0.344	0.332	0.341	0.213	0.004	0.120
Wheat in rotation	2015-2016	Oct. - Dec.	0.425	0.317	0.409	0.157	0.016	0.160
Wheat in rotation	2015-2016	Dec. - Feb.	0.472	0.266	0.370	0.185	0.102	0.081
Wheat in rotation	2015-2016	Feb. - May	0.505	0.347	0.432	0.311	0.073	0.035
Wheat in rotation	2016-2017	Jul. - Oct.	0.498	0.313	0.427	0.272	0.071	0.041
Wheat in rotation	2016-2017	Oct. - Dec.	0.541	0.287	0.292	0.214	0.249	0.073
Wheat in rotation	2016-2017	Dec. - Feb.	0.350	0.284	0.292	0.284	0.059	0.000
Wheat in rotation	2016-2017	Feb. - May	0.424	0.334	0.329	0.287	0.095	0.047
Mean			0.496	0.341	0.436	0.234	0.060	0.107

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Figure S1 - Distribution of the most prevalent proteobacterial genera detected in wheat residues. **(A)** Cladogram of the most prevalent genera. Genera were filtered according to their occurrence (at least three times in five sampling points for each "crop within rotation * cropping season * sampling period" combination). Unclassified genera were removed from the tree. **(B)** Number of ASV for each genus. **(C)** Occurrence of each ASV in the 100 samples of wheat residues. **(D)** Number of reads for each genus. (E) Distribution of each genus in the five samples per date (increasing numbers of reads on a scale running from yellow to red).

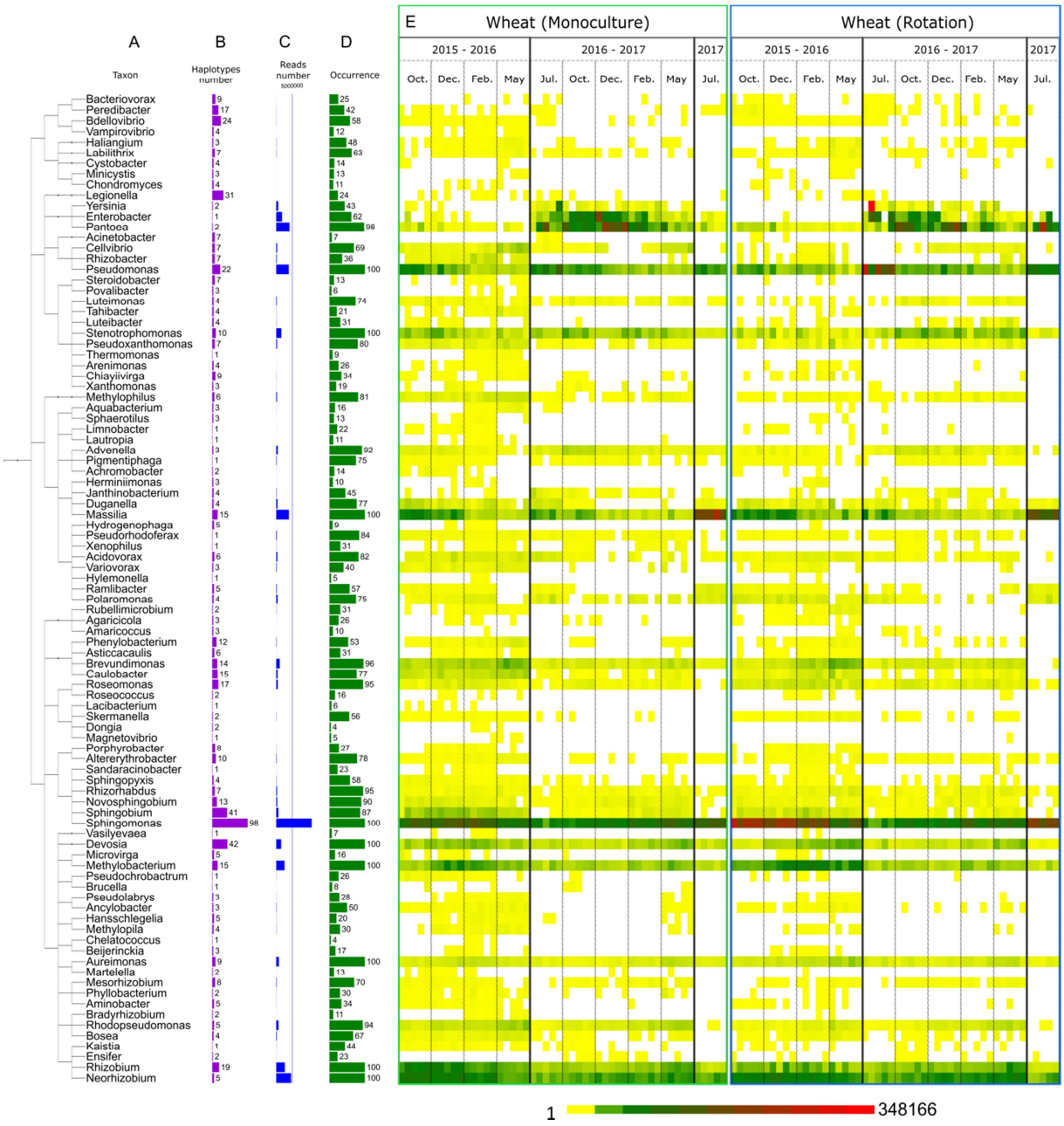

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Figure S2 - Distribution of the most prevalent Actinobacteria, Bacteroides, Firmicutes, Verrucomicrobia, Chlamydiae and Chloroflexi genera detected in wheat residues,. **(A)** Cladogram of the most prevalent genera. Genera were filtered according to their occurrence (at least three times in five sampling points for each "crop within rotation * cropping season * sampling period" combination). Unclassified genera were removed from the tree. **(B)** Number of ASV for each genus. **(C)** Occurrence of each ASV in the 100 samples of wheat residues. **(D)** Number of reads for each genus. **(E)** Distribution of each genus in the five samples per date (increasing number of reads shown on a scale running from yellow to red).

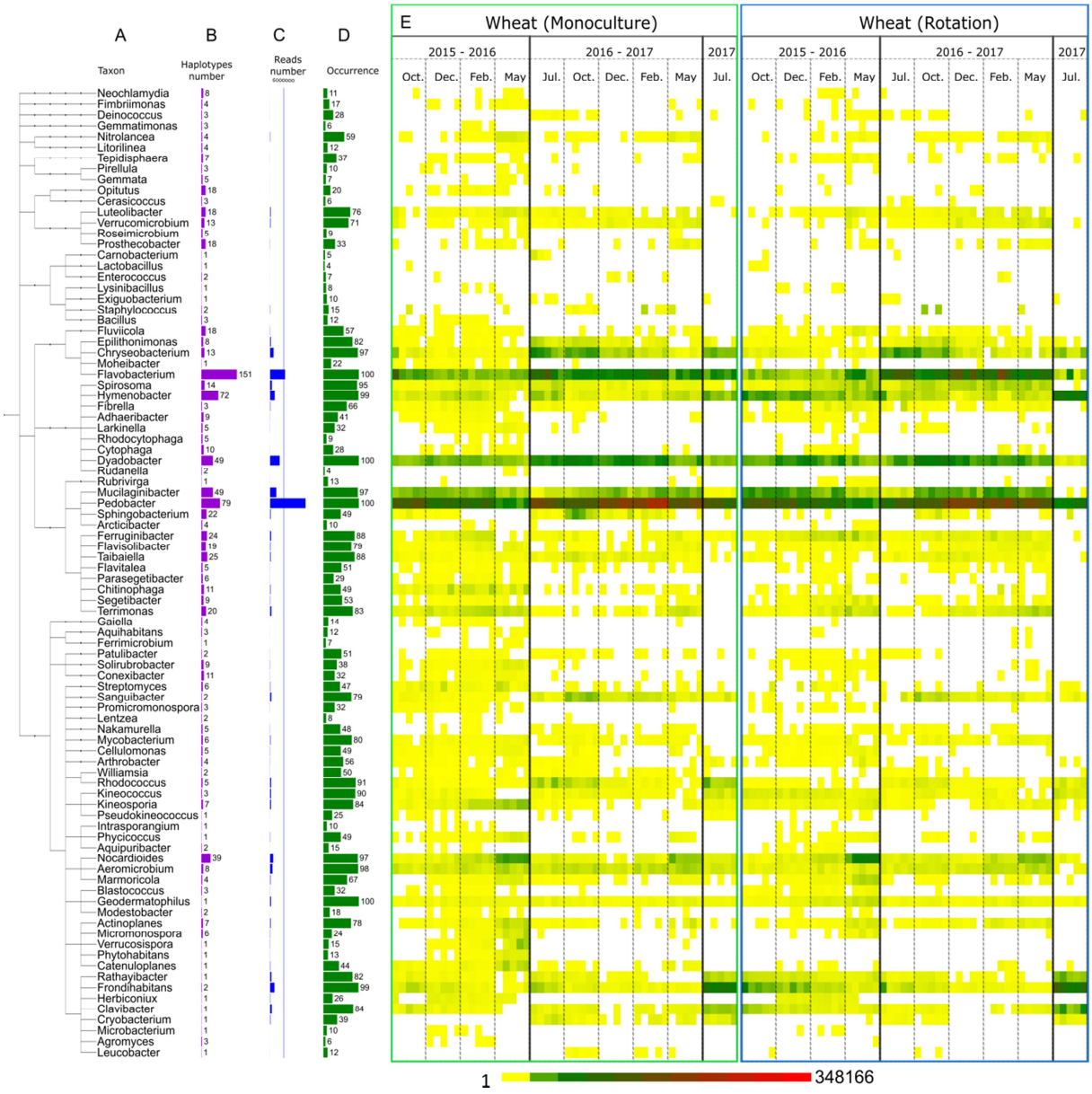

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Figure S3 - Distribution of the most prevalent proteobacterial genera detected in oilseed rape residues. **(A)** Cladogram of most prevalent genera. Genera were filtered according to their occurrence (at least three times in five sampling points for each "crop within rotation * cropping season * sampling period" combination). Unclassified genera were removed from the tree. **(B)** Number of ASV for each genus. **(C)** Occurrence of each ASV in the 49 samples of oilseed rape residues. **(D)** Number of reads for each genus. (E) Distribution of each genus in the five samples per date (increasing number of reads shown on a scale running from yellow to red).

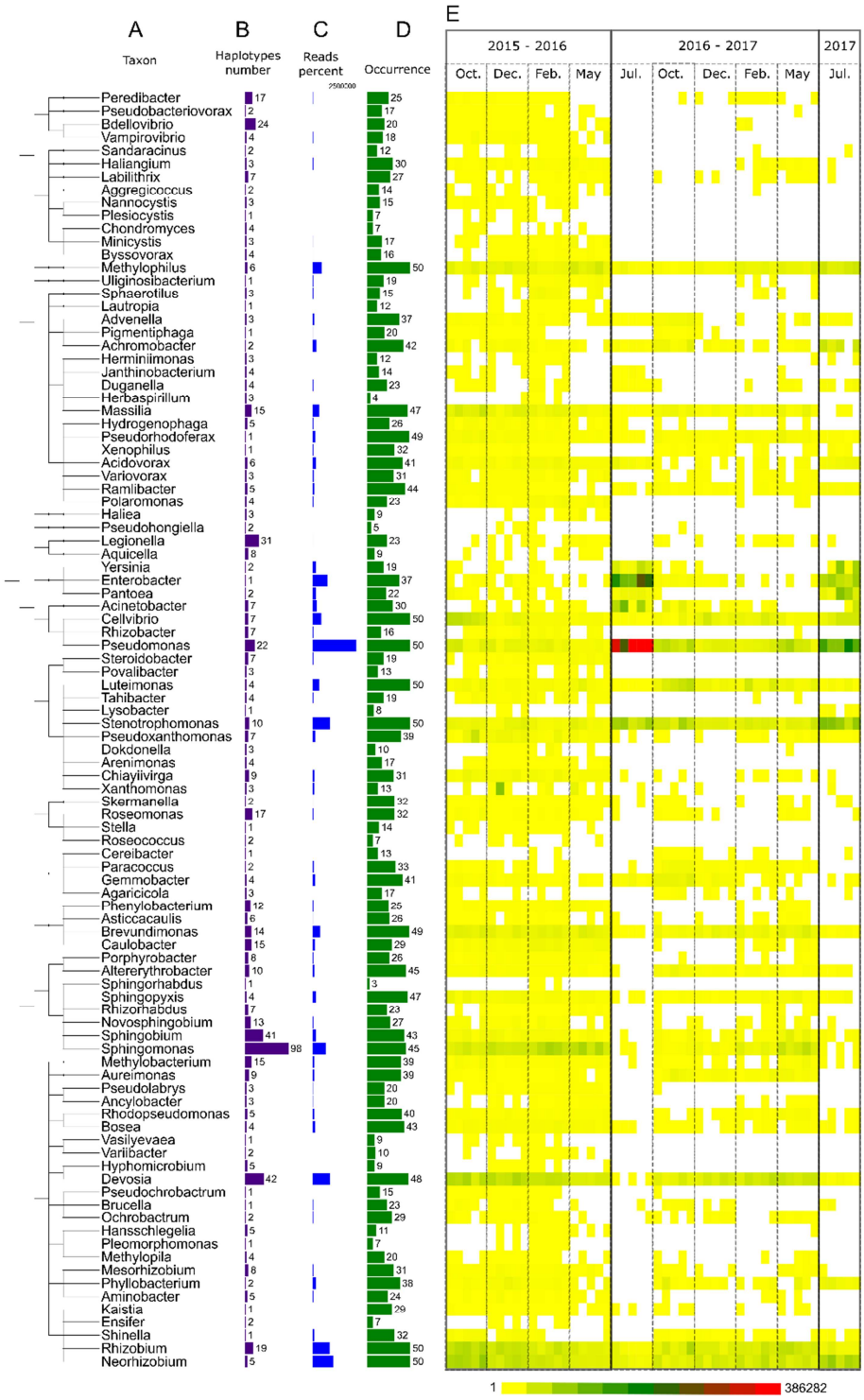

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Figure S4 - Distribution of the most prevalent Actinobacteria, Bacteroides, Firmicutes, Verrucomicrobia, Chlamydiae and Chloroflexi genera detected in oilseed rape residues. **(A)** Cladogram of the most prevalent genera. Genera were filtered according to their occurrence (at least three times in five sampling points for each "crop within rotation * cropping season * sampling period" combination). Unclassified genera were removed from the tree. **(B)** Number of ASV for each genus. **(C)** Occurrence of each ASV in the 49 samples of oilseed rape residues. **(D)** Number of reads for each genus. **(E)** Distribution of each genus in the five samples per date (increasing number of reads shown on a scale from yellow to red).

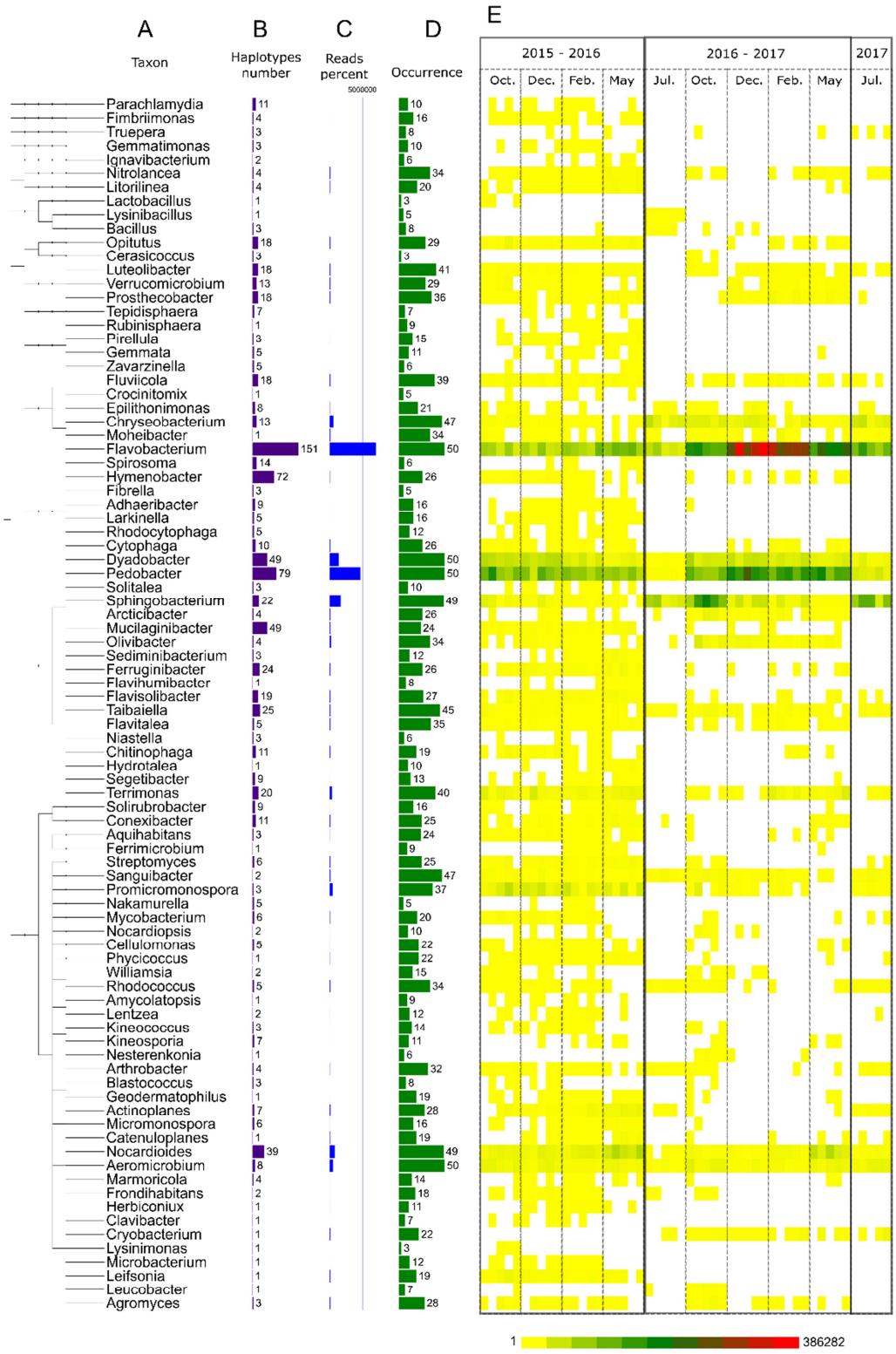

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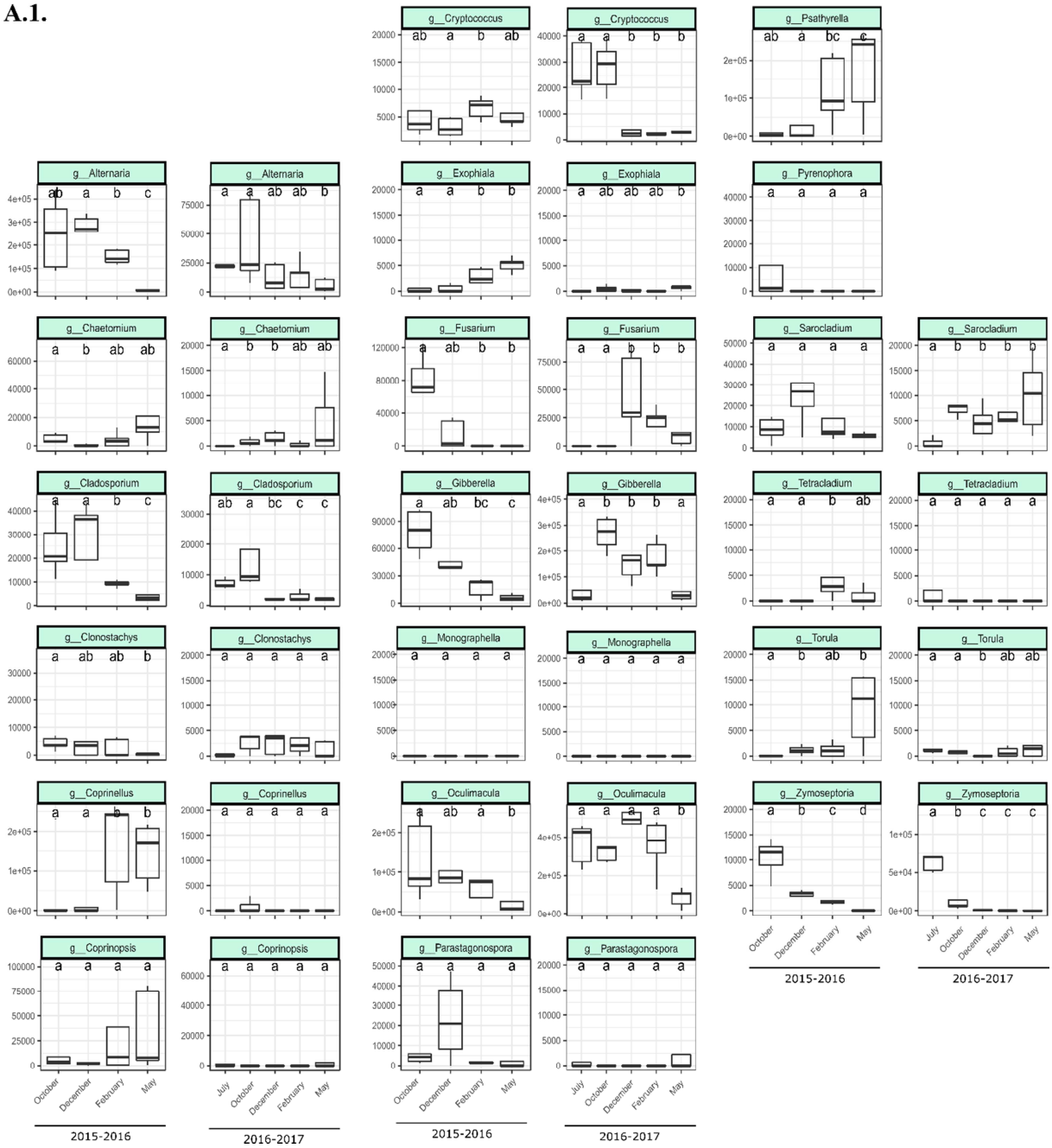
Figure S5 - Seasonal shift in the relative abundance of a selection of fungal **(A)** and bacterial **(B)** genera present on wheat and oilseed rape residues according to the rotation (wheat monoculture **[1]**, wheat in rotation **[2]**, oilseed rape in rotation **[3]**) and the year (2015-2016, 2016-2017). Due to the high impact of the plant (wheat and oilseed rape) in the fungal community, the fungal genera used here as examples are different for the two plants, unlike the case of the bacterial community. Each box represents the distribution of genera relative abundance for the five sampling points. Samples not sharing letters are significantly different (Wilcoxon tests between sampling periods).

A.1.



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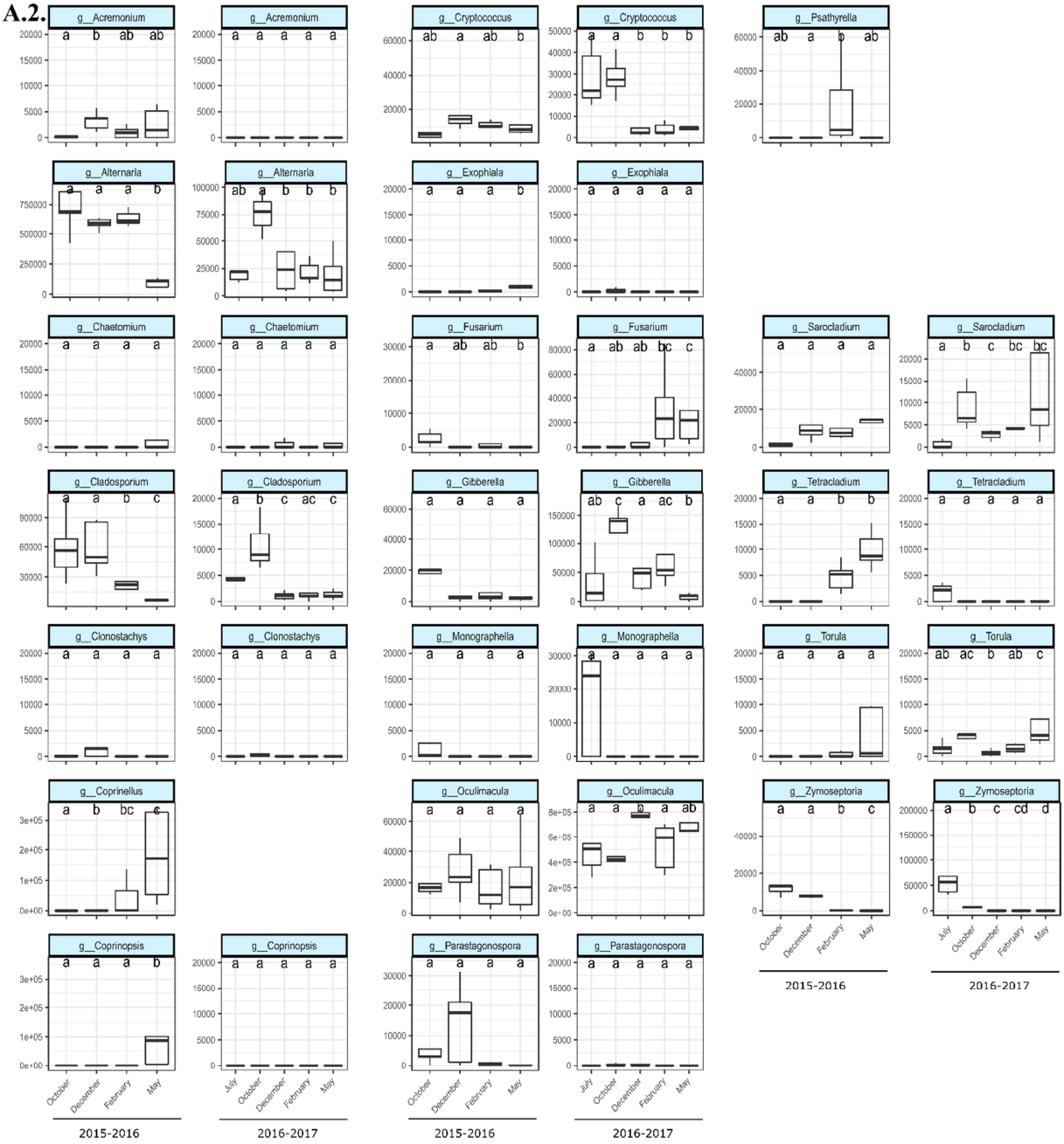
A.2.



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A.3.

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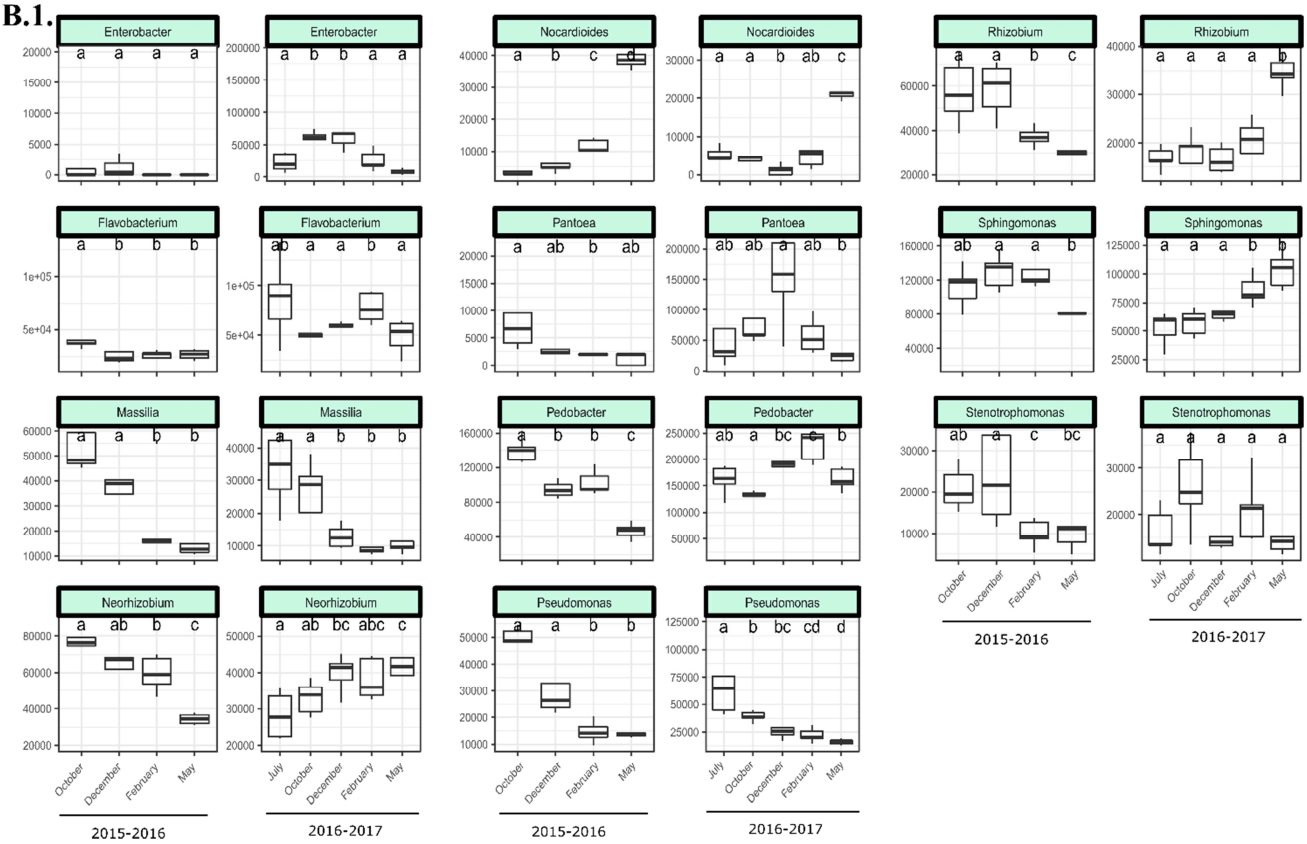
B.1.



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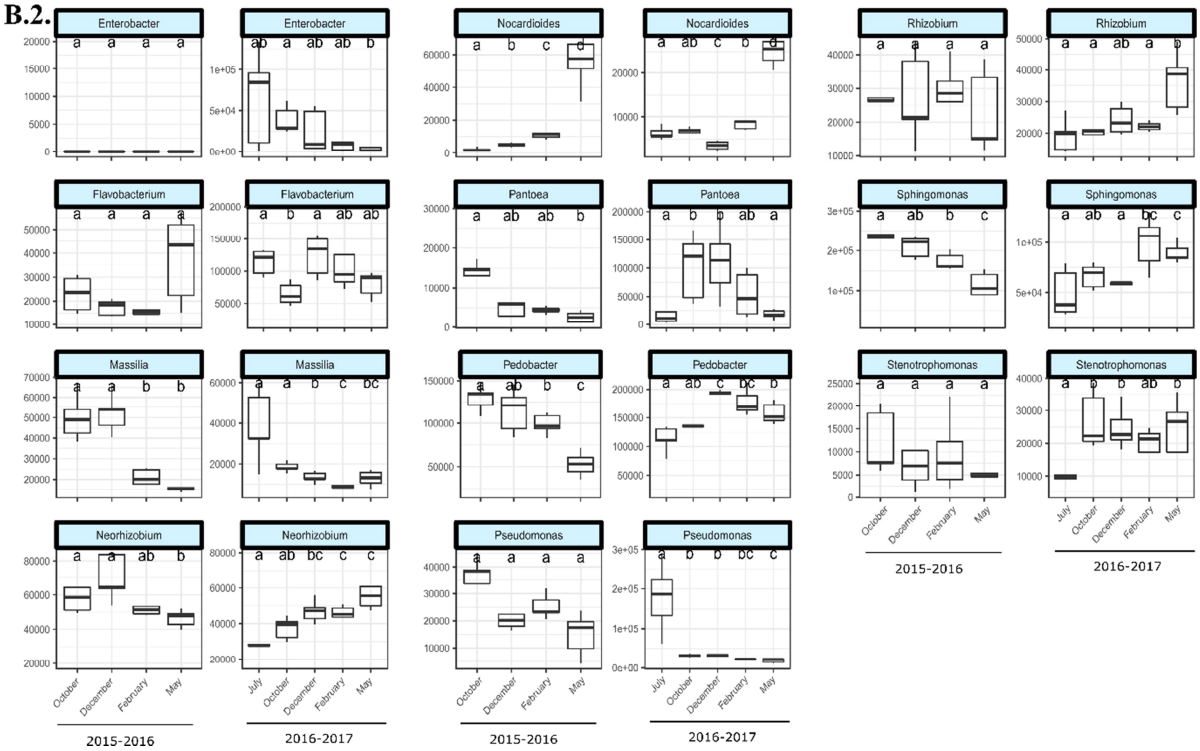
B.2.



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B.3.