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Variability of microbiomes in winter rye, wheat, and triticale affected by snow mold: predicting promising microorganisms for the disease control

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Abstract

Background Snow mold caused by different psychrophilic phytopathogenic fungi is a devastating disease of winter cereals. The variability of the snow mold pathocomplex (the quantitative composition of snow mold fungi) has not been evaluated across different crops or different agrocenoses, and no microbial taxa have been predicted at the whole-microbiome level as potential effective snow mold control agents. Our study aimed to assess the variability of the snow mold pathocomplex in different winter cereal crops (rye, wheat, and triticale) in different agrocenoses following the peak disease progression and to arrange a hierarchical list of microbial taxa predicted to be the main candidates to prevent or, conversely, stimulate the development of snow mold pathogens.

Results The variability of microbiomes between different crops within a particular agrocenosis was largely determined by fungal communities, whereas the variability of microbiomes of a particular crop in different agrocenoses was largely determined by bacterial communities. The snow mold pathocomplex was the most "constant" in rye, with the lowest level of between-replicate variability and between-agrocenoses variability and (similar to the triticale snow mold pathocomplex) strong dominance of *Microdochium* over other snow mold fungi. The wheat snow mold pathocomplex was represented by different snow mold fungi, including poorly investigated *Phoma sclerotioides*. To predict snow mold-control microorganisms, a conveyor of statistical methods was formed and applied; this conveyor enables considering not only the correlation between the abundance of target taxa and a phytopathogen but also the stability and fitness of taxa within plant-associated communities and the reproducibility of the predicted effect of taxa under different conditions. This conveyor can be widely used to search for biological agents against various plant infectious diseases.

Conclusions The top indicator microbial taxa for winter wheat and rye following the winter period were *Ph. sclerotioides* and *Microdochium*, respectively, both of which are causal agents of snow mold disease. Bacteria from the *Cellulomonas*, *Lechevalieria*, and *Pseudoxanthomonas* genera and fungi from the *Cladosporium*, *Entimomentora*,

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Pseudogymnoascus, and *Cistella* genera are prime candidates for testing their plant-protective properties against *Microdochium*-induced snow mold disease and for further use in agricultural practice.

Keywords Plant microbiome, Plant infectious diseases, Snow mold, *Microdochium*, Winter cereal crops, Biological plant disease control

Introduction

The extraction and subsequent use of information hidden in the data on plant-associated microbiomes represent a valuable basis for improving crop performance. Plant-associated microflora significantly determines plant properties, including their productivity [1–4]. In particular, the composition of the microbial community determines plant health and the development of infectious diseases [5, 6].

A devastating disease of winter cereals and grasses, snow mold, develops mostly under snow cover, sometimes causing the almost complete loss of winter cereals [7]. The most common causal agents of snow mold are psychrotolerant/psychrophilic fungi belonging to Ascomycota (*Microdochium nivale*, causing pink snow mold, and *Sclerotinia borealis*, causing snow scald) and Basidiomycota (*Typhula ishikariensis* and *T. incarnata*, causing gray and speckled snow mold, respectively) [8]. Snow mold is predominantly distributed in the Northern Hemisphere (Europe, Canada, the United States, the United Kingdom, and Japan) [9, 10]. Pink snow mold-causing *M. nivale* continuously adapts to warmer weather and shorter winters, allowing snow mold progression in Western and Eastern Europe [7, 11–13]. In addition, *M. nivale* can cause not only snow mold but also other diseases throughout the growing season [14–16]. Snow mold is one of the most difficult-to-manage plant diseases: very few donors of quantitative snow mold resistance are currently used in breeding programmes, whereas the application of fungicides is complicated by the development of snow mold under snow cover [7]. Biocontrol agents, namely microorganisms that suppress snow mold pathogens and stably interact with plants, seem like a potentially promising "tool" for snow mold control. However, except for a single representative of the *Pseudomonas* genus [17, 18], no other potential snow mold-suppressing microorganisms have been described.

Microbiomic data may enable the prediction of particular microorganisms that can serve as effective biocontrol agents against specific diseases [19, 20]. However, the microbiomes of plants following the peak of the parasitic activity of snow mold fungi (after wintering) have not been characterized, except for our previous study, in which the composition of the snow mold-affected winter rye community was analyzed in a particular agrocenosis [21]. This information does not permit analysis of the variability of the snow mold pathocomplex in different crops or prediction of the potential snow mold biocontrol microorganisms.

Potential biocontrol microorganisms have been previously predicted based on microbiome data with regard to several plant diseases other than snow mold: soft rot caused by *Dickeya zeae* in rice [22], Fusarium wilt disease (FWD) caused by *Fusarium oxysporum* in *Musa* spp [23], common scrab caused by *Streptomyces* species in potato [24], FWD caused by *Fusarium* spp. in maize [25], and Fusarium head blight (FHB) caused by *Fusarium* spp. in wheat [26]. The latter is the only study in which biocontrol microorganisms were predicted by the example of winter cereal disease. All of these studies predicted potential biocontrol taxa based on the negative correlation of their content with the content of a particular pathogen. However, these studies did not consider the relative abundance of a microorganism in the total community as a factor that influences its biocontrol properties, despite the fact that this parameter affects the potential antagonistic activity of a microorganism against phytopathogens and reflects its fitness and stability in the plant-associated community. Additionally, the prediction of biocontrol microorganisms was carried out on a particular crop (plant species), whereas many pathogens, including snow mold fungi, affect different crops whose microbiomes are variable, and therefore, the identification of "universal" biocontrol microorganisms for different crops against a particular disease requires analysis of the microbiomes of different crops.

We have set our sights on taking into account these important issues in our study, which was aimed at assessing the variability of the snow mold pathocomplex (as well as microbiomes in general) in different winter cereal crops (rye, wheat, and triticale) in different agrocenoses following peak disease progression and arranging a hierarchical list of microbial taxa predicted to be the main candidates to prevent or, conversely, stimulate the development of snow mold pathogens.

Materials and methods

The experimental model

Microbiomes were analyzed in three winter cereal crops: winter rye (*Secale cereale* L. cv. Ogonek), winter wheat (*Triticum aestivum* L. cv. Nadezhda), and winter triticale (*Triticosecale* Wittm. cv. Kornet); a brief characterization of the cultivars used is provided in the Supplementary file. The crops were grown under field conditions in two agrocenoses located in: (1) Laishevo district of

the Tatarstan Republic, in Bolshiye Kaban (latitude 55.625164 N, longitude 49.351334 E); (2) Arsk district of the Tatarstan Republic, in Nalasa (latitude 56.113468, N, longitude 49.774500 E). The agroclimatic conditions of the Republic of Tatarstan are strongly continental, with long winters and dry spring-summer vegetation. Soil-climatic and agrotechnological conditions differed in the two investigated agrocenoses (for details, see Table S1). In agrocenoses, hereafter referred to as Arsk and Laishevo, snow cover (~ 50 cm deep) is formed in November and remains on average for 183 and 150 days, respectively. Within both agrocenoses, the studied winter cereal crops were planted in competitive variety field trials under uniform agronomic management.

Plant samples were collected one week after snowmelt. Two types of samples were harvested from each plant: (1) roots and (2) dead parts of shoots (DPS) (Fig. 1). In total, 12 sample variants were analyzed (2 agrocenoses × 3 cereal crops × 2 sample types). Within each sample variant, 8 replicates were taken from four randomized 25 m^2-plots of the competitive variety field trials (two replicates per plot). Thus, in total, 96 replicates (12 sample types per 8 replicates) were analyzed. The samples were washed several times with distilled water to remove all soil, then held in 70% ethanol for 10 s, and then washed twice in sterile distilled water. Washed root and DPS samples were frozen in liquid nitrogen and held at -83 °C until use.

DNA extraction, DNA library Preparation and sequencing

Total DNA was extracted from the root and DPS samples using a DNeasy PowerBiofilm Kit (Qiagen, Hilden, Germany) according to the protocol provided by the manufacturer. The quantity of extracted DNA was evaluated

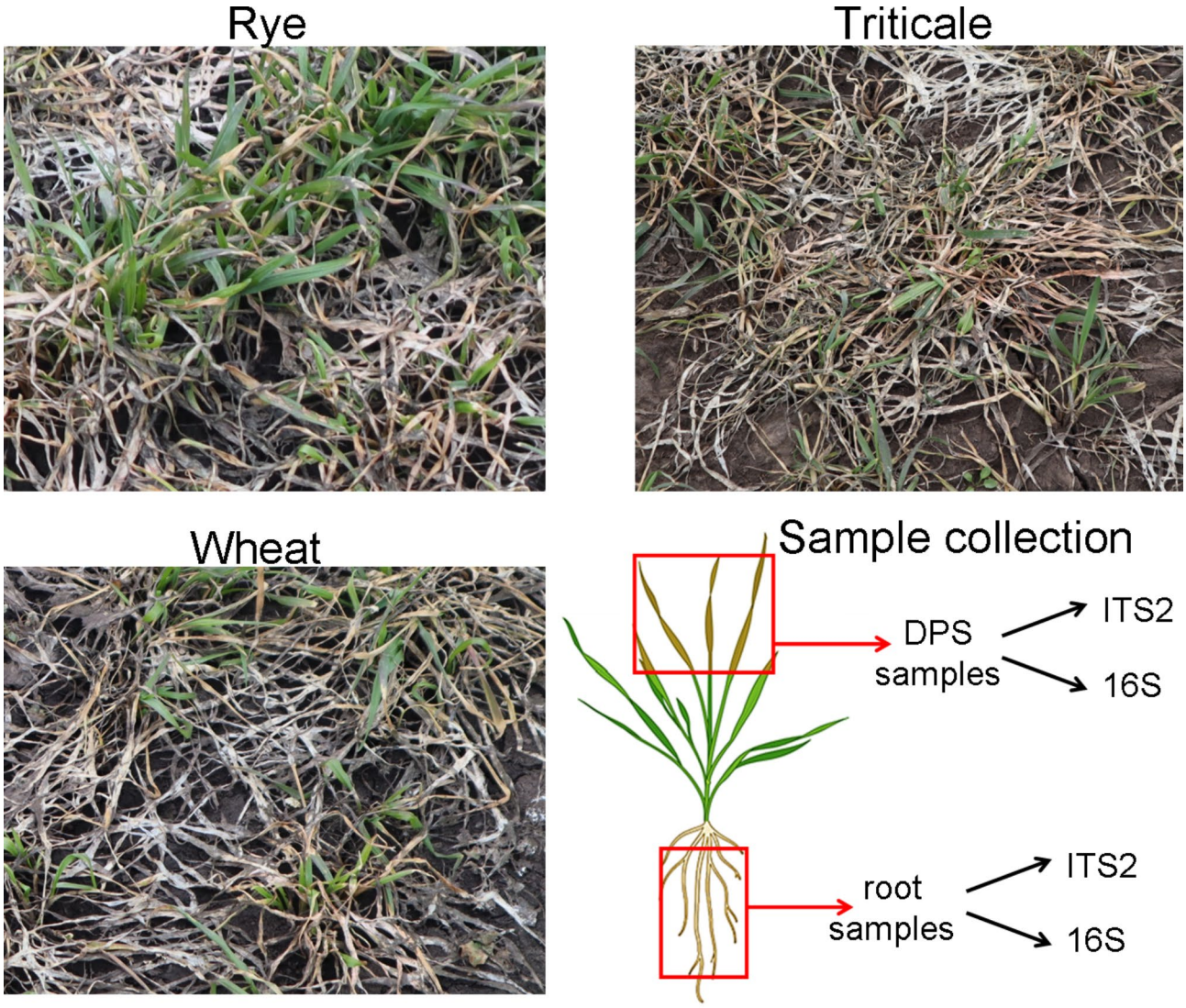


Fig. 1 Winter cereal crops (rye, wheat, and triticale) affected by snow mold and a scheme of sample collection. DPS – dead parts of shoots

using a NanoDrop spectrophotometer (Implen, USA). The ITS2 region of fungal ribosomal RNA (rRNA) was amplified using ITS3_KYO2 (5′–GAT GAA GAA CGY AGY RAA–3′) and ITS4 (5′–TCC TCC GCT TAT TGA TAT GC–3′) primers [27]. The V3 and V4 regions of the 16 S rRNA gene were amplified using the Bakt_341F (5′–CCT ACG GGN GGC WGC AG–3′) and Bakt_805R (5′–GAC TAC HVG GGT ATC TAA TCC–3′) primers [28]. Libraries were prepared according to the Illumina protocol (Illumina protocol, part no. 15044223, Rev. B). The indexing of libraries was performed using the Nextera XT Index Kit v2 (Illumina, USA). Libraries were sequenced on the MiSeq platform using the MiSeq Reagent Kit v3 (600-cycles) (Illumina). All datasets were deposited in the National Center for Biotechnology Information (NCBI) Sequence Reading Archive (SRA) and are available under the PRJNA1154949 bioproject.

Processing of reads and assembly of amplicon sequence variants (ASV)

The obtained reads were processed using FastQC [29], MultiQC [30]), and Cutadapt v.3.5 [31] for quality control and primer sequence removal. The DADA2 [32] pipeline was used for quality trimming, dereplication, filtering for chimeras, and generation of amplicon sequence variants (ASVs). The taxonomic annotation of ASVs was performed against the UNITE v. 8.3 (for fungi) [33] and SILVA (v138) (for bacteria) [34] databases using a naive Bayes classifier, and then the annotation was edited according to the NCBI, Mycobank, and Bacterionet databases. ASVs corresponding to non-fungal or non-bacterial sequences (e.g., chloroplasts, plants, Metazoa) as well as low-abundant ASVs (constituting < 0.00001% of the total fungal or bacterial community) [32, 35] were excluded from further analysis. Good's coverage was calculated using the MicrobiomeAnalyst web resource [36] to evaluate the percentage of diversity obtained by sequencing. Information on the ASV sequences, abundance of ASVs in the analyzed samples, taxonomic annotations of ASVs, and sample sheets describing sample nomenclature are presented on GitHub (https://github.com/ildar-ITS/16S_ITS2_Wheat_Triticale_Rye_DPS_Roots_Microbiome).

Analysis of α- and β-diversity of the communities and variability of the snow mold pathocomplex

α- and β-diversity were analyzed using the MicrobiomeAnalyst web resource [36]. α-Diversity was assessed using the Chao1, Shannon, Gini-Simpson indices; significant differences in the values of indices in pairwise comparisons of samples were determined by the Mann-Whitney test with Benjamini-Hochberg multiplicity correction (FDR < 0.05).

Cumulative sum scaling (CSS) normalization of data was performed for β-diversity analysis [37]. β-Diversity was assessed using principal coordinate analysis (PCoA) based on Bray-Curtis distance; the significance of differences in community structures was assessed using PERMANOVA ($p < 0.05$). The degree and significance of differences in community structures in pairwise comparisons of samples were determined using ANOSIM ($p < 0.05$).

DeSeq2 [38] was used to identify taxa whose relative abundance significantly ($p < 0.05$) differed between samples in pairwise comparisons and to calculate the corresponding Log2FC (logarithm of fold change) values. To identify taxa that contributed most to the variability of microbiomes in pairwise comparisons (taking into account not only differences in the relative abundance of a taxon in the compared samples but also the relative abundance of a taxon in the total community), the Log2FC values for each taxon were weighed by the arcsin-transformed values [39] of the relative abundance (%) of a taxon in the total community (namely, on the geometric mean value of the relative taxon abundance in two compared samples), yielding weighted Log2FC values (W_Log2FC). W_Log2FC values were calculated using XLSTAT 2019.2.2.59614.

To assess the variability/similarity of the snow mold pathocomplex within different samples, box plots, cluster dendrograms, and centroid graphs were plotted in XLSTAT 2019.2.2.59614. Hierarchical agglomerative clustering was performed using Euclidean distance as the distance measure and Ward's method for linkage.

Prediction of taxa that affect *Microdochium*

To predict fungal and bacterial taxa that affected *Microdochium*, considering that both similar and different taxa could affect *Microdochium* in different crops and/or agrocenoses, a dataset of 15 sample groups was created. Within 15 sample groups (differentially 15 for root samples and 15 for DPS samples), 6 samples (Rye_Arsk, Wheat_Arsk, Triticale_Arsk, Rye_Laishevo, Wheat_Laishevo, and Triticale_Laishevo) were combined in a biologically relevant way: all three crops in each particular agrocenosis or in both agrocenoses together (three sample groups), one crop in two different agrocenoses (three sample groups), two crops in pairs in each separate agrocenosis or in two agrocenoses (nine sample groups). The sample groups are listed in Table 1.

Within each of the 15 sample groups, Spearman's correlation coefficients between the relative abundance of each different taxon and the relative abundance of *Microdochium* were determined, and taxa that had a moderate and high significant correlation (Chaddock scale; $r > |0.5|$, t-test, $p < 0.05$) within at least one of the 15 sample groups were selected. Among the selected taxa, those

Table 1 Fifteen sample groups used to predict target taxa (whose relative abundance had a significant weight correlation with the relative abundance of *Microdochium*) using principal component analysis (PCoA). R – rye, W – wheat, T – triticale, A – arsk, L – laishevo, all – all three crops. The first and second letters in the table cells denote the agrocenosis and the crop, respectively. Root samples and samples of dead parts of shoots were analyzed separately

Combination principle	All three crops	Each crop separately	Crops in pairs (Arsk)	Crops in pairs (Laishevo)	Crops in pairs (Arsk and Laishevo)
Set of samples in a sample group	A_All	A_*R*+L_*R*	A_*W*+A_*R*	L_*W*+L_*R*	A_*W*+A_*R*+L_*W*+L_*R*
	L_All	A_*T*+L_*T*	A_*T*+A_*R*	L_*T*+L_*R*	A_*T*+A_*R*+L_*T*+L_*R*
	(L+A)_All	A_*W*+L_*W*	A_*W*+A_*T*	L_*W*+L_*T*	A_*W*+A_*T*+L_*W*+L_*T*

whose relative abundance in the total community was below the critical value (ANOVA) were excluded. For the remaining taxa, the correlation coefficients corresponding to each of the 15 sample groups were weighted by the arcsin-transformed values of the relative abundance (%) of the taxon in the total community (to give priority to more abundant taxa over less abundant taxa within the target prediction). The dataset containing the values of the weighted correlation coefficients for each taxon within all 15 sample groups was used to perform principal component analysis (PCA) to rank the taxa according to the degree of their predicted positive or negative (depending on positive or negative correlation coefficients and on the location of objects (taxa) on the PCA plots relative to the location of vectors) effect on *Microdochium*.

Based on the location of 15 vectors (corresponding to 15 sample groups) on the PCA plot, we selected those biologically compatible sample groups in which target relationships (relationships between the abundance of *Microdochium* and the abundance of different taxa) were more similar (to consider within a common dataset) and in which target relationships were more different (to consider as alternative datasets). Since target relationships (according to the position of vectors) were rather similar within a single agrocenosis, being rather different between different agrocenoses, and were rather similar within rye and triticale samples, being rather different in wheat samples compared to both rye and triticale samples, target taxa with the most pronounced effect on *Microdochium* were searched by PCA within four datasets formed by: (1) all 15 sample groups; (2) sample groups from Arsk (4 sample groups); (3) sample groups from Laishevo (4 sample groups); (4) sample groups containing rye and/or triticale (without wheat) (6 sample groups). For each taxon within each of the four datasets, the sums of the squared cosines of the angles between the objects (taxa) and principal components were determined. According to the values of the sums of squared cosines, a hierarchical list of taxa with the most predicted positive and negative effects on *Microdochium* was arranged within each of the four datasets (differentially for root samples and DPS samples).

Table 2 Sequencing depth and numbers of the revealed amplicon sequence variants (ASVs) and taxa. DPS – dead parts of shoots

	Fungi		Bacteria	
Mean number of high-quality reads per sample	26 305		30 854	
Total number of ASVs*	581		2723	
Good's coverage, %	99.96 ± 0.016		99.33 ± 0.43	
	Roots	*DPS*	*Roots*	*DPS*
Number of ASVs**	486	211	2341	1106
Number of taxa (genus or higher rank)**	172	78	316	181

*Number of ASVs after the removal of the low-abundant ASVs and ASVs corresponding to non-bacterial/non-fungal taxa

**Number of ASVs and number of taxa differentially for root and DPS samples

Results

The composition and α-diversity of fungal and bacterial communities in the roots and DPS of winter cereal crops

Information about the sequencing depth and numbers of the revealed amplicon sequence variants (ASV) and taxa is presented in Table 2.

Among the most represented taxa in both the roots and dead parts of shoots (DPS) were fungi from *Microdochium*, *Cladosporium*, *Vishniacozyma*, *Phaeosphaeria*, *Tetracladium*, *Leptosphaeria*, *Alternaria* genera, and bacteria from *Pseudomonas*, *Cryobacterium*, *Pedobacter*, *Massilia*, *Flavobacterium*, *Duganella*, *Arthrobacter*, *Sphingomonas*, *Pseudarthrobacter*, *Rhizobium* genera (Fig. 2). Among the most represented taxa in roots were also fungi from *Pseudogymnoascus*, *Cistella*, *Fusarium*, *Ophiosphaerella*, *Entimomentora*, *Nectria*, *Mortierella*, *Prosthemium*, *Alpinaria*, *Schizothecium* genera, and bacteria from *Devosia*, *Streptomyces*, *Nocardioides*, *Actinoplanes*, *Cellulomonas*, *Promicromonospora*, *Galbitalea*, *Knoellia* genera, whereas fungi from *Sclerotinia*, *Dioszegia*, *Neoascochyta*, *Typhula*, *Itersonilia*, *Helgardiomyces*, *Zymoseptoria*, *Oculimacula*, *Epiccocum*, *Mrakia*, *Rhexocercosporidium* genera, and bacteria from *Conyzicola*, *Frigoribacterium*, *Janthinobacterium*, *Leifsonia*, *Paeniglutamicibacter*, *Rhodococcus*, *Chryseobacterium*, *Agreia*, *Aeromicrobium*, *Aureimonas* genera were also among the most represented taxa in DPS (Fig. 2).

α-Diversity (Chao1, Shannon, Gini-Simpson indices) was compared in biologically relevant sample pairs: (1)

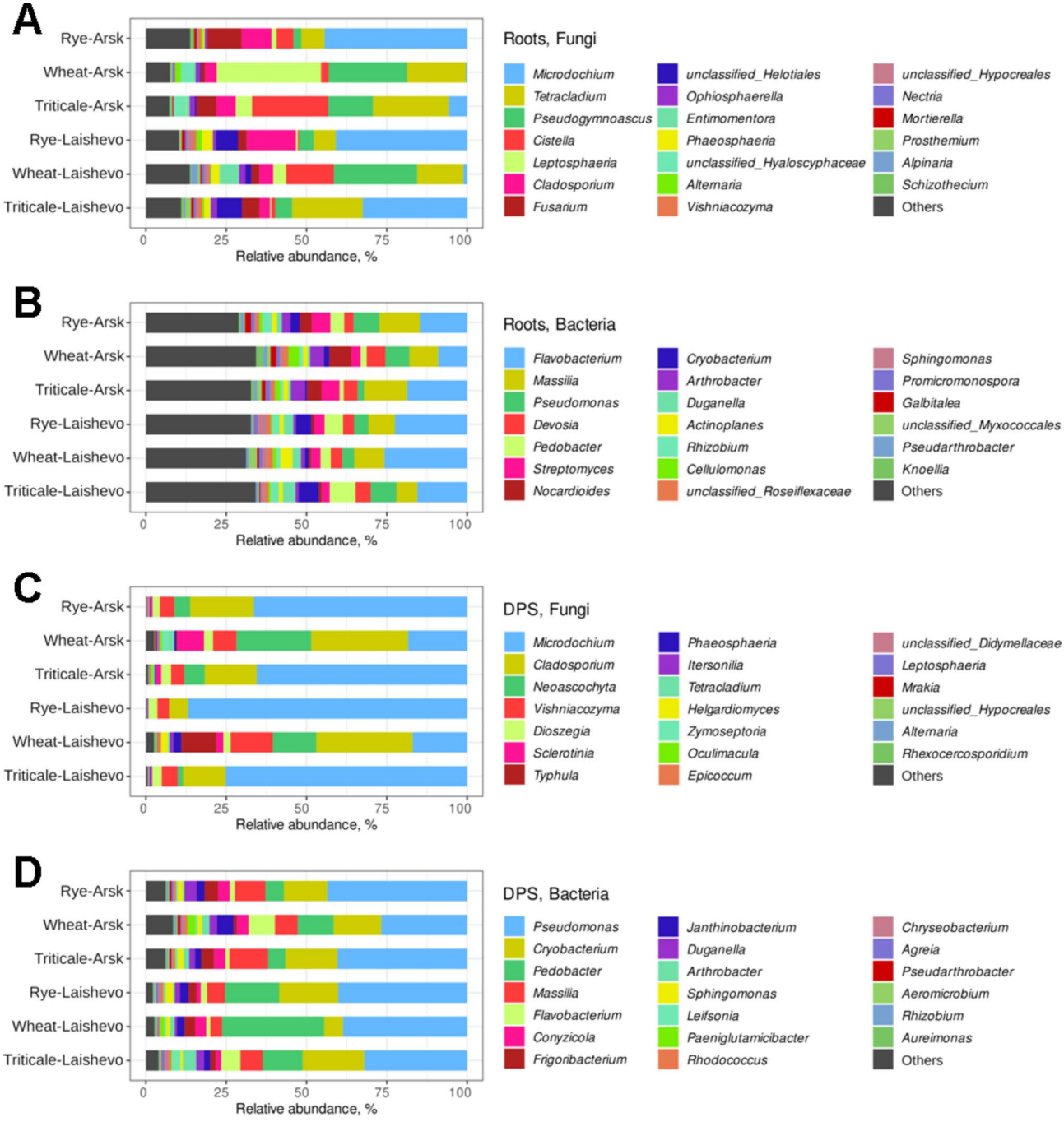


Fig. 2 Percentage of top-20 taxa (genera) of fungi and bacteria in microbial communities of roots and dead parts of shoots (DPS) of winter cereal crops (rye, wheat, and triticale) grown in different agrocenoses (Laishevo, Arsk). **A** fungi in roots, **B** bacteria in roots, **C** fungi in DPS, **D** bacteria in DPS

the communities of one crop in different agrocenoses (3 pairs of comparison); (2) the communities of two crops in one agrocenosis (6 pairs of comparison: three for one agrocenosis and three for the other); (3) the communities of roots and DPS within a particular crop and particular agrocenosis (6 pairs of comparison).

For fungal communities, the values of all three α-diversity indices were higher in root samples than in DPS samples, except that the values of the Chao1 indices in wheat DPS samples were higher than those in wheat root samples (Table S2). For bacterial communities, the Chao1 indices in the samples of all three crops were significantly higher in root samples than those in the DPS samples. Thus, we observed a tendency for a higher α-diversity of the root microbial communities than in DPS microbial communities.

The pairwise comparison (medians and significance of their difference) of Chao1, Shannon, and Gini-Simpson indices in a particular crop in different agrocenoses and different crops in a particular agrocenosis is presented in Table 3; the corresponding box charts are presented in Figure S1. The α-diversity of both the fungal and bacterial communities of roots was dependent on the conditions of agrocenosis. For fungal communities, the values of the Chao1 indices in the samples of all three crops from Laishevo were higher than those from Arsk, whereas for the bacterial community, in contrast, all three α-diversity indices in the samples of all three crops from Arsk were higher than those from Laishevo (Table 3). In different crops, the conditions of agrocenosis differentially affected the α-diversity of the fungal root community: the Chao1 index in wheat was the highest in Laishevo and the lowest in Arsk compared to that in rye and triticale in the respective agrosenoses (Table 3). Within a particular agrocenosis, the assayed crop type had only a small (if any) effect on the α-diversity of the root bacterial community: no significant differences in the α-diversity of the bacterial community between crops were revealed in Arsk samples, and only some differences were found in Laishevo samples (Table 3).

Within DPS samples, when comparing a particular crop in different agrocenoses, fungal communities differed in terms of α-diversity indices only in the samples of rye (but not wheat and triticale) (Table 3). Within each separate agrocenosis, the values of all three α-diversity indices for fungal communities were significantly highest in wheat samples (compared to those in rye and triticale samples), whereas the lowest values were observed in rye samples. For DPS bacterial communities, the values of the Chao1 index in the samples of all three crops from Arsk were higher than those from Laishevo, indicating that the α-diversity of the DPS bacterial community was dependent on the conditions of agrocenosis. Within each separate agrocenosis, the values of all three α-diversity indices for bacterial communities did not differ in the samples of different crops (except that the Shannon index in wheat samples from Arsk was higher than that in rye samples from Arsk) (Table 3). Thus, we observed a tendency for the type of crop to have a greater influence on the α-diversity of the root and DPS fungal communities (compared to the influence of the type of agrocenosis) and for the type of agrocenosis to have a greater influence on the α-diversity of the root and DPS bacterial communities (compared to the influence of the type of crop).

Table 3 Comparison of Chao1, Shannon, and Gini-Simpson indices reflecting the α-diversity of fungal and bacterial communities of roots and dead parts of shoots (DPS) of winter cereal crops (rye, wheat, and triticale) grown in different agrocenoses (Laishevo, Arsk). The particular pairwise comparison is indicated in the column "Comparison pair". R – rye, W – wheat, T – triticale, A – arsk, L – laishevo. Each cell in the table contains two values corresponding to the medians of the indices for a particular comparison pair. The Italic background shows a significant difference (Mann–Whitney test with Benjamini—Hochberg multiplicity correction, $p < 0.05$, FDR < 0.05) within a comparison pair. The corresponding box charts are presented in figure S1

Comparison group	Comparison pair	Fungi			Bacteria		
		Chao1	Shannon	Gini-Simpson	Chao1	Shannon	Gini-Simpson
Roots							
One crop in two agrocenoses	**W_A vs. W_L**	*65 vs. 131*	*2.5 vs. 3.2*	*0.84 vs. 0.92*	*1025 vs. 576*	*5.5 vs. 5.0*	*0.99 vs. 0.97*
	T_A vs. T_L	*78 vs. 95*	2.9 vs. 3.0	0.91 vs. 0.89	*882 vs. 521*	*5.2 vs. 4.7*	*0.99 vs. 0.97*
	R_A vs. R_L	*76 vs. 99*	2.6 vs. 2.4	0.85 vs. 0.80	*978 vs. 486*	*5.4 vs. 4.4*	*0.99 vs. 0.94*
Different crops in Arsk	**W_A vs. R_A**	*65 vs. 76*	2.5 vs. 2.6	0.84 vs. 0.85	1025 vs. 978	5.5 vs. 5.4	0.99 vs. 0.99
	W_A vs. T_A	*65 vs. 78*	*2.5 vs. 2.9*	*0.84 vs. 0.91*	1025 vs. 882	5.5 vs. 5.2	0.99 vs. 0.99
	R_A vs. T_A	76 vs. 78	2.6 vs. 2.9	*0.85 vs. 0.91*	978 vs. 882	5.4 vs. 5.2	0.99 vs. 0.99
Different crops in Laishevo	**W_L vs. R_L**	*131 vs. 99*	*3.2 vs. 2.4*	*0.92 vs. 0.80*	*576 vs. 486*	*5.0 vs. 4.4*	0.97 vs. 0.94
	W_L vs. T_L	*131 vs. 95*	3.2 vs. 3.0	0.92 vs. 0.89	*576 vs. 521*	5.0 vs. 4.7	0.97 vs. 0.97
	R_L vs. T_L	99 vs. 95	2.4 vs. 3.0	0.80 vs. 0.89	486 vs. 521	*4.4 vs. 4.7*	0.94 vs. 0.97
Dead parts of shoots (DPS)							
One crop in two agrocenoses	**W_A vs. W_L**	79 vs. 78	2.1 vs. 2.3	0.80 vs.0.83	*514 vs. 230*	*4.2 vs. 3.1*	0.95 vs. 0.87
	T_A vs. T_L	58 vs. 55	1.6 vs. 1.5	0.70 vs.0.66	*424 vs. 288*	3.6 vs. 3.6	0.93 vs. 0.93
	R_A vs. R_L	*49 vs. 39*	*1.4 vs. 1.0*	*0.63 vs.0.46*	*504 vs. 239*	3.7 vs. 3.2	0.93 vs. 0.89
Different crops in Arsk	**W_A vs. R_A**	*79 vs. 49*	*2.1 vs. 1.4*	*0.80 vs.0.63*	514 vs. 504	*4.2 vs. 3.7*	0.95 vs. 0.93
	W_A vs. T_A	*79 vs. 58*	*2.1 vs. 1.6*	*0.80 vs.0.70*	514 vs. 424	4.2 vs. 3.6	0.95 vs. 0.93
	R_A vs. T_A	49 vs. 58	1.4 vs. 1.6	0.63 vs.0.70	504 vs. 424	3.7 vs. 3.6	0.93 vs. 0.93
Different crops in Laishevo	**W_L vs. R_L**	*78 vs. 39*	*2.3 vs. 1.0*	*0.83 vs.0.46*	230 vs. 239	3.1 vs. 3.2	0.87 vs. 0.89
	W_L vs. T_L	*78 vs. 55*	*2.3 vs. 1.5*	*0.83 vs.0.66*	230 vs. 288	3.1 vs. 3.6	0.87 vs. 0.93
	R_L vs. T_L	*39 vs. 55*	*1.0 vs. 1.5*	*0.46 vs.0.66*	239 vs. 288	3.2 vs. 3.6	0.89 vs. 0.93

β-diversity of fungal and bacterial communities in the roots and DPS of winter cereal crops

The analysis of the β-diversity revealed that wheat and rye root mycobiomes were partitioned into non-overlapping PcoA clusters (that was observed for each separate agrocenosis). The clusters of wheat samples in different agrocenoses overlapped as well as clusters of rye samples in different agrocenoses (Fig. 3). In contrast, triticale root mycobiomes in different agrocenoses were partitioned into non-overlapping PcoA clusters. Herewith, triticale mycobiomes from Arsk and Laishevo overlapped, respectively, with wheat mycobiome from Arsk and with rye mycobiome from Laishevo. ANOSIM tests confirmed that (1) triticale root mycobiomes in different agrocenoses were more variable than wheat and rye mycobiomes in different agrocenoses; (2) in each assayed agrocenosis, of the three pairwise comparisons of the three crops` root mycobiomes, wheat and rye mycobiome structures were the most variable; (3) in Arsk, the triticale root mycobiome resembled more the wheat root mycobiome than the rye mycobiome, whereas in Laishevo, it resembled more the rye mycobiome than the wheat mycobiome (Fig. 3). The obtained results showed that the structures of the assayed root mycobiomes were determined more by the type of crop than by the type of agrocenosis. The exception was the triticale community, in which root mycobiome structure was significantly determined by the type of agrocenosis and had rather low variability compared with either rye or wheat root mycobiome structures (depending on the agrocenosis).

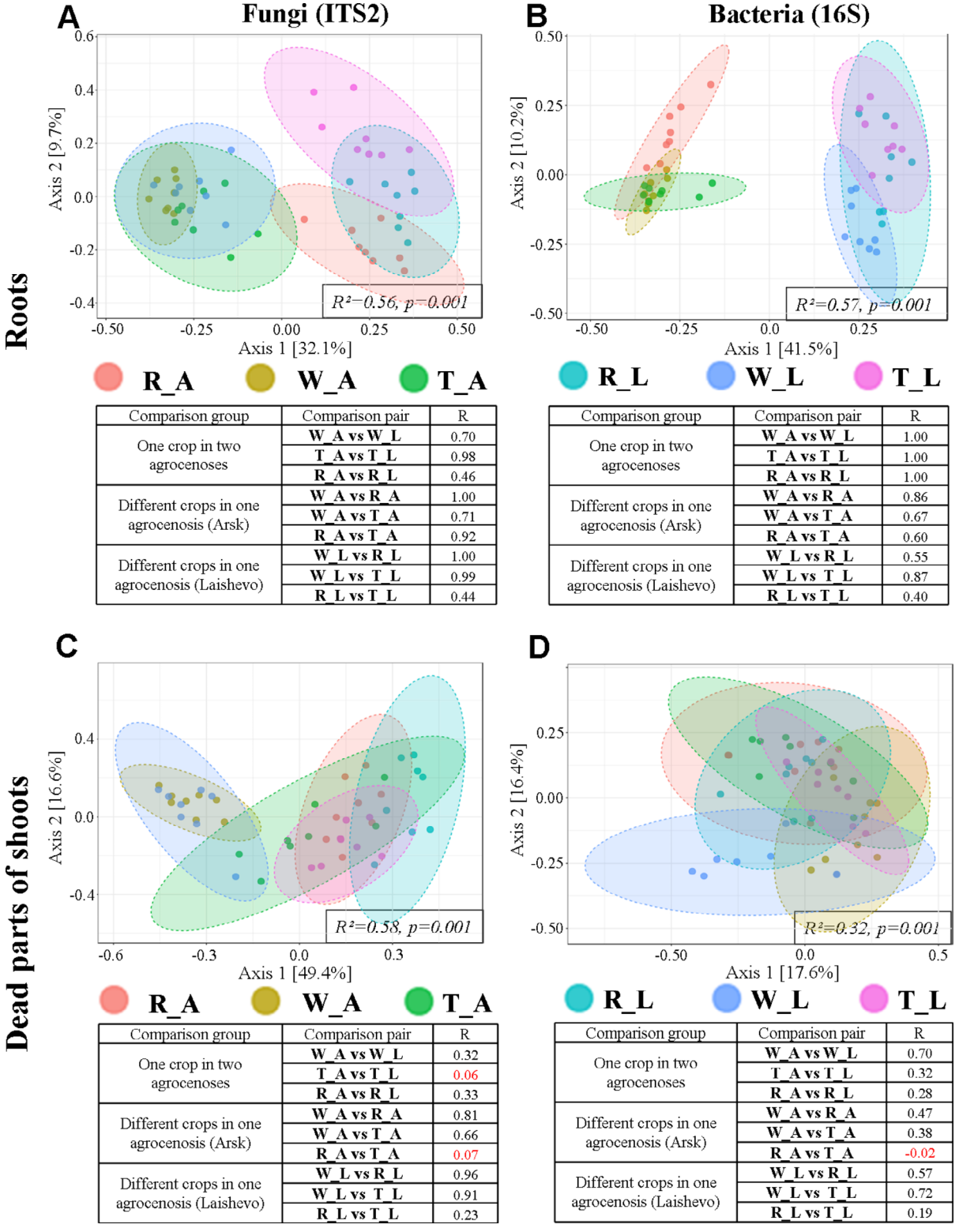
The PcoA clusters of the assayed root bacterial microbiomes were split into non-overlapping groups depending on the type of agrocenosis. Within these groups, the samples of the three crops (within a common agrocenosis) clustered together, with the majority of overlap (Fig. 3). This means that the type of agrocenosis (but not the crop type) plays a dominant role in the determination of the structure of root bacterial communities. According to the ANOSIM tests, the rye and triticale communities showed the smallest differences in root bacterial microbiome structures in both agrocenoses (Fig. 3).

Wheat and rye DPS mycobiomes were partitioned into non-overlapping PcoA clusters (that was observed for each separate agrocenosis). The clusters of wheat samples from different agrocenoses overlapped as did clusters of rye and triticale samples from different agrocenoses (Fig. 3). Herewith, the cluster corresponding to the DPS mycobiome of triticale grown in Arsk overlapped with all other five clusters, whereas the cluster corresponding to the DPS mycobiome of triticale grown in Laishevo overlapped with the rye mycobiome clusters. Thus, the structures of the assayed DPS mycobiomes (as well as root mycobiomes) were determined more by crop type than by agrocenosis type. This was confirmed by ANOSIM tests that showed that (1) each separate crop was characterized by small (rye and wheat) or no (triticale) differences in the bacterial DPS mycobiome structures in different agrocenoses; (2) of the three pairwise comparisons of the three crops` DPS mycobiomes, wheat and rye mycobiome structures were the most variable, whereas the mycobiomes of rye and triticale were the least variable (in Laishevo) or even displayed no significant variability (in Arsk) (Fig. 3).

All six PcoA clusters of the assayed DPS bacterial microbiomes overlapped with each other, indicating that DPS bacterial microbiomes in different winter cereal crops were rather conservative under different agrocenoses (Fig. 3). ANOSIM tests showed that (1) wheat DPS bacterial microbiomes were more variable in different agrocenoses than those of rye and triticale; (2) of the three pairwise comparisons of the three crops` DPS bacterial microbiomes, the microbiomes of rye and triticale were the least variable (in Laishevo) or even displayed no significant variability (in Arsk) (Fig. 3).

We further identified taxa that made the most significant contribution to the variability of the assayed microbiomes. Herewith, we relied on the calculated values of W_Log2FC (the weighted logarithm of fold change) that combined two parameters: the logarithm of fold change in relative taxon abundance in two samples (Log2FC) and the relative abundance (%) of the taxon in microbial communities. Taking the latter parameter into account increases the significance of higher abundant taxa over less abundant taxa in terms of their contribution to the variability of microbiomes. The full list of taxa with significant Log2FC values and corresponding W_Log2FC values in pairwise comparisons (one crop in two agrocenoses or two crops in a particular agrocenosis) is presented in Table S3. The top-5 taxa with the highest W_Log2FC values and the top-5 taxa with the lowest W_Log2FC values for each comparison pair are presented in Table S4.

Among the revealed top-5 taxa (Table S4), the weighted abundance (W_Log2FC values) of *Pedobacter*, *Actinocorallia*, *Rhizorhabdus*, *Sphingomonas*, *Rhizobium* (bacteria), and *Cladosporium* (fungi) was higher in rye roots compared to both wheat and triticale roots in one of two agrocenoses (either Arsk or Laishevo); herewith, the weighted abundance of *Microdochium* was higher in rye compared to wheat in both agrocenoses simultaneously and also compared to triticale from Arsk. The weighted abundance of *Knoellia*, *Phycicoccus*, *Arenimonas*, *Frigoribacterium*, *Actinoplanes*, unidentified *Myxococcales* (bacteria), *Pseudogymnoascus*, *Cistella*, and *Entimomentora* (fungi) was higher in wheat roots compared to both rye and triticale roots in one of two agrocenoses; herewith, the weighted abundance of *Leptosphaeria* was higher in wheat compared to both rye and triticale in both



Comparison group	Comparison pair	R
One crop in two agrocenoses	W_A vs W_L	0.70
	T_A vs T_L	0.98
	R_A vs R_L	0.46
Different crops in one agrocenosis (Arsk)	W_A vs R_A	1.00
	W_A vs T_A	0.71
	R_A vs T_A	0.92
Different crops in one agrocenosis (Laishevo)	W_L vs R_L	1.00
	W_L vs T_L	0.99
	R_L vs T_L	0.44

Comparison group	Comparison pair	R
One crop in two agrocenoses	W_A vs W_L	1.00
	T_A vs T_L	1.00
	R_A vs R_L	1.00
Different crops in one agrocenosis (Arsk)	W_A vs R_A	0.86
	W_A vs T_A	0.67
	R_A vs T_A	0.60
Different crops in one agrocenosis (Laishevo)	W_L vs R_L	0.55
	W_L vs T_L	0.87
	R_L vs T_L	0.40

Comparison group	Comparison pair	R
One crop in two agrocenoses	W_A vs W_L	0.32
	T_A vs T_L	0.06
	R_A vs R_L	0.33
Different crops in one agrocenosis (Arsk)	W_A vs R_A	0.81
	W_A vs T_A	0.66
	R_A vs T_A	0.07
Different crops in one agrocenosis (Laishevo)	W_L vs R_L	0.96
	W_L vs T_L	0.91
	R_L vs T_L	0.23

Comparison group	Comparison pair	R
One crop in two agrocenoses	W_A vs W_L	0.70
	T_A vs T_L	0.32
	R_A vs R_L	0.28
Different crops in one agrocenosis (Arsk)	W_A vs R_A	0.47
	W_A vs T_A	0.38
	R_A vs T_A	-0.02
Different crops in one agrocenosis (Laishevo)	W_L vs R_L	0.57
	W_L vs T_L	0.72
	R_L vs T_L	0.19

Fig. 3 Principal coordinate analysis (PCoA) based on Bray-Curtis distance of the fungal (**A**, **C**) and bacterial (**B**, **D**) communities of roots (**A**, **B**) and dead parts of shoots (DPS) (**C**, **D**) of winter cereal crops (rye, wheat, and triticale) grown in different agrocenoses (Laishevo, Arsk). R – rye, W – wheat, T – triticale, A – Arsk, L – Laishevo. The color legend for the ellipses (representing 95% confidence intervals) is given at the bottom of the PcoA plots. Tables below the PcoA plots show R values (ANOSIM, $p < 0.05$) for pairwise microbiome comparisons: the communities of one crop in different agrocenoses (3 pairs of comparisons) and the communities of two crops in one agrocenosis (6 pairs of comparisons: three for one agrocenosis and three for the other). Black and red values in the tables indicate significant (black) and insignificant (red) differences (ANOSIM, $p < 0.05$) within a comparison pair

agrocenoses simultaneously (Table S4). The revealed *Leptosphaeria*-related ASVs corresponded to *Leptosphaeria sclerotioides* (teleomorph) or *Phoma sclerotioides* (anamorph), which has been proposed to be a causal agent of snow mold [40, 41]. Therefore, *Ph. sclerotioides* was further considered in our study as one of the snow mold-causal agents, along with *Microdochium*, *Typhula*, and *Sclerotinia*.

The weighted abundance of *Actinocorallia*, *Lechevalieria*, *Nonomuraea* (bacteria), and *Cistella* (fungi) was higher in triticale roots compared to both wheat and rye roots in one of two agrocenoses (either Arsk or Laishevo); in both agrocenoses simultaneously, none of the taxa had a higher weighted abundance in triticale roots compared to wheat and rye roots (Table S4). The weighted abundance of *Nocardioides*, *Arthrobacter* (bacteria), *Neoascochyta*, and unidentified *Helotiales* (fungi) differed in each of the three crops depending on the agrocenosis (Table S4); these taxa may thus be considered determinants of the variability of the cereal microbiome under different growth conditions.

In DPS, the taxa whose weighted abundance was higher in one crop compared to both other crops in one of the agrocenoses (but not in both agrocenoses simultaneously) were revealed: the weighted abundance of *Cladosporium*, *Dioszegia*, and *Aureobasidium* (fungi) was higher in rye, *Flavobacterium*, *Conyzicola*, unidentified *Solirubrobacteraceae*, unidentified *Oxalobacteraceae* (bacteria), *Tetracladium*, *Leptosphaeria*, *Typhula*, *Phaeosphaeria*, *Neoascochyta* (fungi) in wheat, and unidentified *Didymellaceae* (fungi) in triticale. The weighted abundance of *Pseudarthrobacter* and *Nocardioides* (bacteria) was higher in one agrocenosis compared to the other in each of the three crops (Table S4).

The structure of the pathocomplex of snow mold in winter cereals

Then we assessed the variability of the snow mold pathocomplex, namely, the quantitative composition of the snow mold fungi (*Microdochium*, *Typhula*, *Sclerotinia borealis*, *Phoma sclerotioides*), in different winter cereal crops in different agrocenoses. In the rye roots of both agrocenoses, *Microdochium* clearly dominated over other snow mold fungi, as well as in the roots of triticale from Laishevo (Fig. 4). In the roots of triticale from Arsk, *Microdochium* and *Ph. sclerotioides* were equally represented, while the total abundance of snow mold fungi was lower than in the roots of triticale from Laishevo. The lowest level of snow mold fungi was observed in the roots of wheat from Laishevo, where *Microdochium*, *Ph. sclerotioides*, and *Typhula* were equally represented. The only sample type in which the clear dominance of non-*Microdochium* snow mold fungi was revealed was wheat from Arsk, where *Ph. sclerotioides* dominated (Fig. 4).

To analyze whether sample replicates were consistent with each other in terms of the quantitative composition of snow mold fungi and to assess the hierarchy of variability in different samples, hierarchical clustering of sample-to-sample Euclidean distances was performed. Within root samples, the most represented first cluster included replicates where *Microdochium* strongly dominated over other snow mold fungi: all 16 rye replicates from both agrocenoses and all 8 replicates of triticale from Laishevo (Fig. 4). The second and third clusters together (that were closer to each other than each of them to the first cluster) included all 16 wheat replicates from both agrocenoses and all 8 replicates of triticale from Arsk. The second cluster included 7 of 8 replicates of wheat from Arsk, where *Ph. sclerotioides* strongly dominated, while the third cluster included the rest of the samples in which snow mold fungi were rather poorly represented by *Microdochium* and *Ph. sclerotioides* in relatively equal proportions (Fig. 4).

In DPS, *Microdochium* strongly dominated (constituting 60–90% of the total fungal community) in rye and triticale samples from both agrocenoses. In the DPS of wheat, the relative abundance of snow mold fungi was lower than that of rye and triticale (Fig. 4). In the DPS of wheat from Laishevo, *Microdochium* and *Typhula* were equally represented, whereas in wheat from Arsk, where *Microdochium* was the most represented, a significant proportion of *Sclerotinia* was also revealed. No significant abundance of *Ph. sclerotioides* was revealed in DPS, even in wheat from Arsk, where *Ph. sclerotioides* dominated over other snow mold fungi in root samples. Hierarchical clustering divided the analyzed 48 DPS replicates into three clusters. The first minor cluster included 13 out of 16 wheat replicates, which were rather poorly represented by snow mold fungi and in which the proportion of *Microdochium* was slightly increased compared to *Typhula* and *Sclerotinia*. The second and third clusters, in which *Microdochium* strongly dominated, included all triticale and rye replicates as well as three wheat replicates. The performed analysis revealed a tendency for the division of replicates into second and third clusters with respect to the agrocenosis from which replicates were collected: 14 of 16 replicates from Arsk constituted the second cluster, whereas 15 of 19 replicates from Laishevo constituted the third cluster (Fig. 4).

Prediction of microbial taxa that can potentially inhibit or stimulate the development of *Microdochium nivale* in the roots and dead shoots of winter cereal crops

Given that *Microdochium* was the most represented snow mold fungus in the analyzed samples, based on the target microbiome profiles, we attempted to predict taxa that could potentially inhibit or stimulate this phytopathogen. Herewith, we relied on the calculated values of weighted

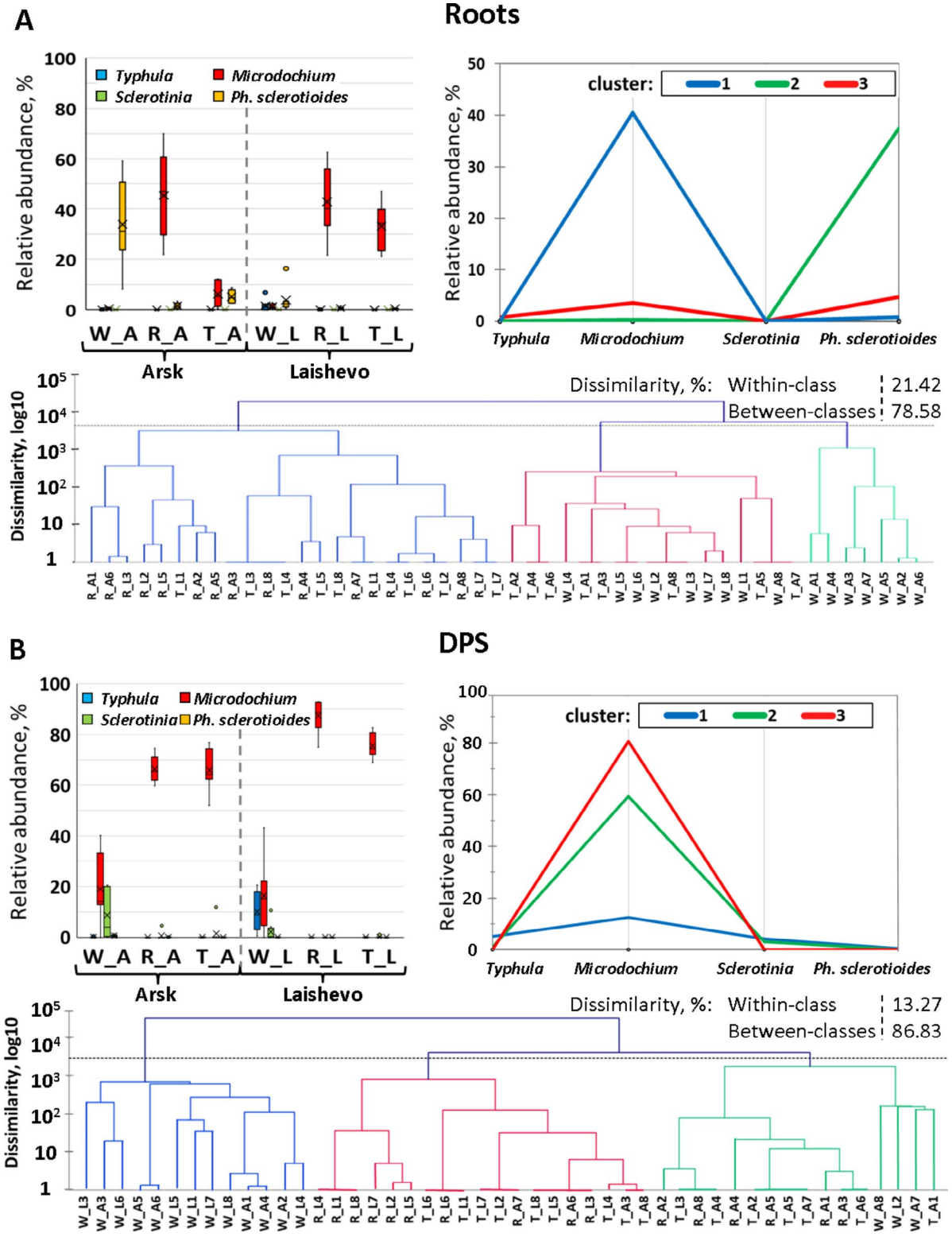


Fig. 4 Variability/similarity of the snow mold pathocomplex (the quantitative composition of the snow mold fungi (*Microdochium*, *Typhula*, *Sclerotinia borealis*, *Phoma sclerotioides*)) in roots (**A**) and dead parts of shoots (DPS) (**B**) of different winter crops (rye, wheat, triticale) in different agrocenoses (Arsk, Laishevo). Box plots show the relative abundance of snow mold fungi (*Microdochium* (red boxes), *Typhula* (blue boxes), *Sclerotinia borealis* (green boxes), *Phoma sclerotioides* (yellow boxes)) in different samples. The dendrograms show hierarchical agglomerative clustering of samples based on the pathocomplex structure using Euclidean distance as the distance measure and Ward's method for linkage. Centroid plots show the relative representation of snow mold fungi for each cluster. R – rye, W – wheat, T – triticale, A – Arsk, L – Laishevo

Spearman's correlation coefficients that combined two parameters: (1) the correlation coefficient between the relative abundance of a particular taxon and the relative abundance of *Microdochium*, and (2) the relative abundance (%) of a taxon in microbial communities. Weighting the correlation coefficient allowed us to consider relative abundance as a factor that contributes to the manifestation of the potential phytopathogen-restricting or phytopathogen-stimulating properties of a taxon and reflects its fitness and stability in the plant-associated microbial community.

Since the relationships between the abundance of particular taxa may differ among crops and agrocenoses, the prediction of target taxa (whose abundance had a significant weight correlation with the abundance of *Microdochium*) was performed in different sample groups using principal component analysis (PCA) (differentially for root and DPS samples). For this, 6 samples (Rye_Arsk, Wheat_Arsk, Triticale_Arsk, Rye_Laishevo, Wheat_Laishevo, and Triticale_Laishevo) were combined into 15 sample groups, where samples were grouped in a biologically relevant way: all three crops in each particular agrocenosis or in both agrocenoses together (three sample groups), one crop in two different agrocenoses (three sample groups), two crops in pairs in each separate agrocenosis or in two agrocenoses (nine sample groups). The sample groups are listed in Table 1.

The abundance of 202 and 114 taxa in root and DPS samples, respectively, correlated ($r > |0.5|$, $p < 0.05$) with the abundance of *Microdochium* at least in one of the 15 sample groups (Table S5). Removal of taxa whose abundance was below the critical value (ANOVA) reduced the list of target taxa to 153 and 62 for root and DPS samples, respectively. For these taxa, weighted correlation coefficients were calculated for each of the 15 sample groups (Table S6), and the resulting dataset was used for PCA.

The PCA results showed that the vectors corresponding to sample groups within each individual agrocenosis were mostly more closely located to each other on the PCA plot than the vectors corresponding to sample groups between agrocenoses (Fig. 5). This means that target relationships (weighted correlation between taxon abundance and *Microdochium* abundance) had much more in common in different experimental groups within a particular agrocenosis than in different agrocenoses. Such a tendency was observed for the samples of both roots and DPS (Fig. 5). In addition, within root samples, a vector corresponding to a sample group consisting of only wheat samples was separated from most of the other vectors, indicating that the target relationships were the most specific in wheat than in rye and triticale (Fig. 5). These PCA results were in accordance with the results of the β-diversity analysis.

Based on the PCA results, we then predicted taxa whose abundance was most closely related to the abundance of *Microdochium*, considering the possible variability of the target relationships among different sample groups. Among these taxa, we searched for the most "universal" ones, namely those for which target relationships were similar in all (most) sample groups, including those that were the most different in terms of the target relationships in general. For this, we analyzed the location of objects (taxa) in PCA plots generated using four datasets formed by: (1) all 15 sample groups (Fig. 5); (2) sample groups from Arsk (4 sample groups) (Figure S2); (3) sample groups from Laishevo (4 sample groups) (Figure S2); (4) sample groups that included rye and/or triticale (without wheat) (6 sample groups) (Figure S2). To create a hierarchical list of taxa according to their effect (positive or negative in accordance with the positive or negative correlation of their abundance with the abundance of *Microdochium*) on *Microdochium*, the sums of squared cosines of the angles between the objects (taxa) and principal components were determined for each taxon within each of the four datasets.

Among the 153 and 62 taxa in root and DPS samples, respectively, that presumably affected *Microdochium* (had non-zero values of the weighted correlation coefficient in at least one of the 15 sample groups), the top-25% taxa (with the highest values of the sums of squared cosines) were determined within each of the four datasets. Then, the top-25% taxa from the four datasets were combined into a common list (differentially for root and DPS samples and differentially for taxa with predicted positive and negative effects on *Microdochium*) that contained 78 and 29 taxa for root and DPS samples, respectively (Table S7). Among these taxa, 51 taxa (15 fungal and 36 bacterial) negatively affected and 27 taxa (6 fungal and 21 bacterial) positively affected *Microdochium* in roots, whereas 17 taxa (12 fungal and 5 bacterial) negatively affected and 12 taxa (2 fungal and 10 bacterial) positively affected *Microdochium* in DPS (Table S7). The effect of most of these taxa on *Microdochium* abundance was predicted in one-two of the four datasets, indicating that this predicted effect was significantly dependent on crop type and/or agrocenosis (Table S7). However, the list of top-25% taxa also included such taxa whose predicted effect on *Microdochium* was manifested within all four or three of the four datasets (Table 4), indicating that the possible effect of these taxa on *Microdochium* was "stable", i.e., it was not dependent (or weakly dependent) on the type of crop and/or agrocenosis. Among the top taxa with a predicted negative effect on *Microdochium* were *Cellulomonas*, *Pseudoxanthomonas*, *Lechevalieria*, *Leptosphaeria* (*Ph. sclerotioides*), *Entimomentora*, *Pseudogymnoascus*, *Cistella* (in roots), *Neoascochyta*, and *Neoascochyta* (in DPS), whereas *Rhodococcus*, *Rhizorhabdus*,

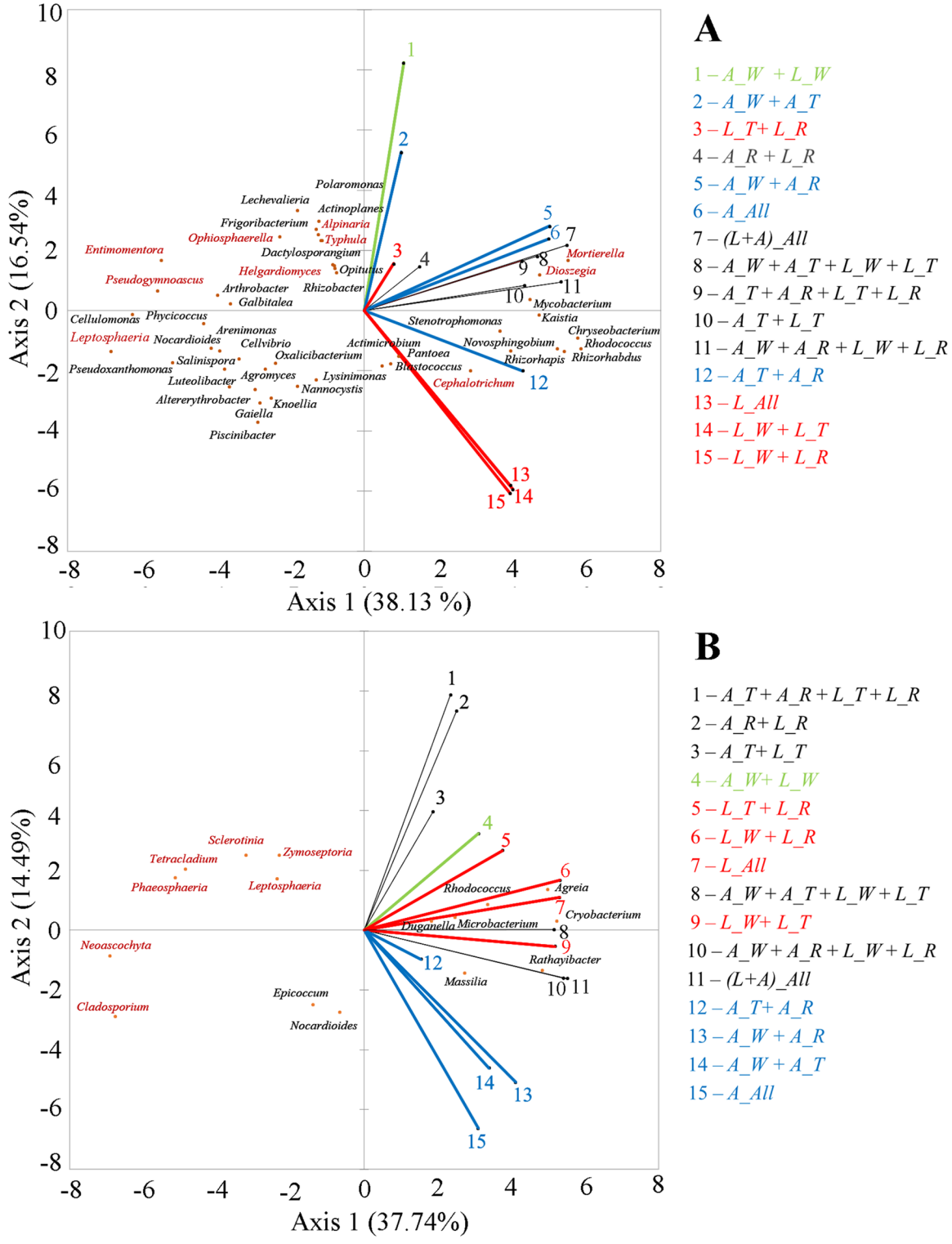


Fig. 5 Visualization of the results of PCA based on Euclidean distance plotted using a dataset of weighted Spearman's correlation coefficients between the abundance of different taxa and the abundance of *Microdochium* in roots (**A**) and dead parts of shoots (**B**) of different winter cereal crops (rye, wheat, triticale) in different agrocenoses (Arsk, Laishevo). R – rye, W – wheat, T – triticale, A – Arsk, L – Laishevo, All – all three crops. Vectors display 15 sample groups combined from 6 samples (Rye_Arsk, Wheat_Arsk, Triticale_Arsk, Rye_Laishevo, Wheat_Laishevo, and Triticale_Laishevo) in a biologically relevant manner; the 15 sample groups are deciphered in Table 1. Red vectors correspond to the sample groups of the "Laishevo" category (containing only samples from Laishevo); blue vectors correspond to the sample groups of the "Arsk" category; and green vectors correspond to the sample groups of the "Wheat" category. Objects (taxa) are designated by dots with taxon names: black—bacteria; brown—fungi

Table 4 Microbial taxa predicted (using the PCA) to have the most reproducible negative (green background) or positive (yellow background) effect on *Microdochium* in the roots and dead parts of shoots (DPS) of winter cereal crops. For each taxon, values in cells are the sums of squared cosines of the angles between the objects (taxa) and principal components determined within four datasets formed by: (1) all 15 sample groups; (2) sample groups from Arsk; (3) sample groups from Laishevo; (4) sample groups that include rye and/or triticale (without wheat). Sample groups are deciphered in Table 1. The table includes only those taxa that had the highest (top-25%) values of the sums of squared cosines within all four (red numbers) or three of four (black numbers) datasets. Bacterial taxa are marked in black, fungal taxa are marked in blue

	Sums of squared cosines			
	Whole dataset	Arsk	Laishevo	Rye+Triticale
Top-taxa predicted to have a negative effect on *Microdochium* in roots				
Cellulomonas	0.980	0.997	0.996	0.982
Pseudoxanthomonas	0.938	0.993		0.984
Lechevalieria	0.704	0.988	0.986	0.720
Leptosphaeria (*Ph. sclerotioides*)	0.902		0.998	0.986
Entimomentora	0.866	0.992	0.998	0.980
Pseudogymnoascus	0.853	0.999	0.999	0.717
Cistella		0.988	0.999	0.822
Top-taxa predicted to have a positive effect on *Microdochium* in roots				
Rhodococcus	0.955	0.995	0.993	0.957
Rhizorhabdus	0.922	0.991		0.774
Chryseobacterium	0.909	0.993		0.947
Top-taxa predicted to have a negative effect on *Microdochium* in DPS				
Neoascochyta	0.849	0.996	1.000	0.885
Cladosporium	0.796		0.998	0.965
Top-taxon predicted to have a positive effect on *Microdochium* in DPS				
Cryobacterium	0.809		0.805	0.999

Chryseobacterium (in roots), and *Cryobacterium* (in DPS) were predicted to have the most reproducible positive effect on *Microdochium* (Table 4).

Discussion

Our study is the first to compare the fungal and bacterial microbiomes in different winter cereal crops after wintering, when a devastating disease, snow mold, progresses. The microbiomes of the three assayed winter cereal crops (rye, wheat, and triticale), namely the phyllosphere fungal communities, have been previously compared in only one study [42], while the microbiomes of two of the three assayed crops (rye and triticale) have been previously analyzed in only a few studies [21, 42–44]. No microbiomes of cereals were analyzed after wintering, except for our previous study on winter rye [21].

In this study, root microbiomes and the microbiomes of dead parts of shoots (DPS) were characterized by using a conveyor of methods widely accepted for analyzing plant microbiomes [20, 22–24, 26, 43, 44]. Root microbiomes were more variable in different crops and under different agrocenoses than DPS microbiomes. This is consistent with the fact that DPS communities composed of saprotrophic microorganisms were characterized by lower α-diversity compared to root communities composed mainly of symbiotic microorganisms. Furthermore, the higher variability of root communities compared to DPS communities is likely related to the fact that the former, in contrast to the latter, are affected by host plant responses, which might have differences among different crops, providing conditions for increased variability of root microbial communities.

The variability of microbiomes (both root and DPS) between different crops within a particular agrocenosis was largely determined by the mycobiome, whereas the bacterial community made a small contribution to the variability of microbiomes between different crops. Rye and wheat mycobiomes were the most different in pairwise comparison of three crops` mycobiomes, whereas triticale mycobiomes had much in common with the mycobiomes of either rye or wheat depending on the agroceniosis. In turn, the variability of the root microbiomes of a particular crop under different agrocenoses was largely determined by the bacterial communities,

whereas the mycobiomes of a particular crop under different agrocenoses had low variability.

Previously, in a number of studies comparing both fungal and bacterial microbiomes in different plant species or under different growth conditions, it was also observed that growth conditions contributed more to the variability of the bacterial microbiome, whereas in different plant species, fungal communities were more variable than bacterial communities [20, 25, 45]. Studies in which only either mycobiomes or bacterial microbiomes were analyzed also showed that the structures of fungal communities were mostly determined by host plant species rather than agrocenosis, whereas the structures of bacterial communities were mostly determined by growth conditions rather than host plant species [42, 46, 47]. This indicates that fungal communities are characterized by more pronounced elements of host specificity than bacterial communities. In turn, the bacterial communities within a particular crop are rather "flexible" and are strongly affected by host plant growth conditions. Therefore, it is reasonable to presume that it is the bacterial "part" of the plant-associated microbial community that provides the "fine-tuning" of plants to the conditions of particular agrocenosis. Herewith, this kind of "fine-tuning" has much in common in different plant species since bacterial communities in different crops within a particular agrocenosis are characterized by low variability. However, it should be noted that opposite situations when the structures of bacterial communities were mostly determined by the host plant species but not by the growth conditions of the host plant were also described [48, 49].

We then determined the taxa that contributed the most to the variability of microbiomes in different crops, namely those taxa whose weighted abundance was higher in one crop compared to the other. The weighted abundance of most of these taxa was higher in one crop compared to one or two others but only in one of the two agrocenoses. The most obvious indicator taxa were *Ph. sclerotioides*, which predominated in wheat compared to both rye and triticale in both agrocenoses, and *Microdochium*, which predominated in rye compared to wheat in both agrocenoses, as well as triticale in one of the two agrocenoses.

Ph. sclerotioides is not as widely known as a snow mold causal agent as *Microdochium*, *Typhula*, and *Sclerotinia* species. However, *Ph. sclerotioides* is known to inhabit cool climate regions and cause plant disease at -2 – +4 °C [40]; therefore, it has been attributed to a snow mold causal agent [41]. The emergence of *Ph. sclerotioides* among the top indicator taxa in winter wheat affected by snow mold following wintering, as shown in our study, indicates that this fungal species indeed should be further considered and studied as a snow mold causal agent.

Although *Microdochium* appeared to be the most obvious indicator taxon of winter rye, i.e., its weighted abundance was higher in rye compared to both wheat and triticale, snow mold manifestation during sample collection was less pronounced in rye than in wheat and triticale. This is in accordance with the fact that rye is considered the most snow mold-resistant winter cereal crop [7, 50]. This indicates that more intensive plant colonization by *Microdochium* is not necessarily associated with more intensive snow mold development. Therefore, it is reasonable to presume that during interactions with rye plants, *Microdochium* fungi act in a "more mutualistic" way than they act in wheat and triticale, where they utilize "more parasitic" behavior. Such differential behavior of *Microdochium* fungi can be explained by the phenotypic heterogeneity of *Microdochium* strains. In our previous study, we showed that *Microdochium nivale* strains inhabiting particular agrocenosis differed in their virulence from highly virulent to almost completely avirulent [21]. Thus, it is possible that the discrepancy between the level of *Microdochium* abundance and the level of snow mold progression is related to the colonization of different crops by phenotypically distinct strains of this fungus. Verification of this assumption requires the identification of genetic markers of phenotypic traits in *Microdochium*, and the recently performed assembly and annotation of the first *M. nivale* genome provide a basis for solving this task [51].

Snow mold can be caused by different fungi (*Microdochium*, *Typhula*, *Sclerotinia*, and *Ph. sclerotioides*), constituting the snow mold pathocomplex [7, 8, 41]. In our study, we assessed the variability/similarity of the snow mold pathocomplex in different winter crops in different agrocenoses. Hierarchical clustering of the samples showed that among the analyzed crops, the composition of the root snow mold pathocomplex was the most "constant" in rye, where the lowest level of between-replicate variability and between-agrocenoses variability was revealed. In rye and triticale, *Microdochium* strongly dominated over other snow mold fungi. Wheat was the only assayed crop where *Ph. sclerotioides* could strongly dominate (under particular conditions) over other snow mold fungi.

The DPS snow mold pathocomplex was similar in rye and triticale, with strong dominance of *Microdochium*. Herewith, rye and triticale DPS replicates were divided into two different clusters depending not on the crop type but on the type of agrocenosis. This indicates that the agrocenosis conditions contributed to some variability in the low-variable rye and triticale DPS snow mold pathocomplex. In wheat DPS, snow mold fungi were relatively poorly represented (compared to the DPS of rye and triticale), and the wheat DPS snow mold pathocomplex in the background of *Microdochium* predominance contained

significant amounts of *Typhula* and *Sclerotinia*. Interestingly, despite the fact that in wheat roots from Arsk, *Ph. sclerotioides* strongly dominated, only trace amounts of *Ph. sclerotioides* were revealed in the samples of wheat DPS from Arsk, where *Microdochium* and *Sclerotinia* constituted almost the entire pool of snow mold fungi. Presumably, this can be related to the possible preference of *Ph. sclerotioides* for a more biotrophic lifestyle, whereas other snow mold fungi are known to combine biotrophic, necrotrophic, and saprophytic lifestyles [8].

Based on the obtained microbiome profiles, we attempted to predict taxa that restricted or, in contrast, contributed to the thriving of the major snow mold causal agent *Microdochium*. Here, as in several other studies on other crops and other diseases [22, 23, 25, 26, 52], we relied on the correlation between taxon abundance and *Microdochium* abundance. In addition, for the identification of target taxa (that potentially affected *Microdochium*), we considered two parameters that are important for reliable prediction of such taxa. First, we considered the relative abundance of a microorganism in the total community as a factor that influences the manifestation of its properties and reflects its stability in the plant-associated community. Second, we searched for taxa whose abundance had similar target relationships (namely, whose abundance had a similar weight correlation with *Microdochium* abundance) within different datasets in order to reveal the microorganisms that might have similar influence on *Microdochium* under different conditions (different crops, different agrocenoses), particularly conditions where the target relationships were the most different. The proposed algorithm for predicting microbial taxa with target properties can be widely used, and, particularly, it (based on appropriate data on microbiome profiles) can contribute to the search for taxa that can protect various plant species from different infectious diseases.

We found that within the whole dataset, samples from different agrocenoses were characterized by the most different target relationships. Besides, the target relationships in wheat were the most specific among the three assayed crops. Therefore, we searched for the target taxa within four datasets: the whole dataset, datasets for each agrocenosis separately, and a dataset from which wheat samples were excluded. Within each dataset, we determined the taxa that had the most pronounced effect on *Microdochium*. The ratio between the number of fungal taxa and bacterial taxa (fungi/bacteria) was higher within those taxa that negatively affected *Microdochium* than within taxa that positively affected *Microdochium*; such a tendency was especially pronounced within DPS samples. This means that, in general, fungi cause more negative effects on *Microdochium* than they cause positive effects, whereas bacteria cause more positive effects on *Microdochium* than they cause negative effects.

The abundance of many taxa that were predicted to affect *Microdochium* had target relationships with *Microdochium* abundance within the dataset from only one of two agrocenoses. For example, a number of taxa were predicted to affect *Microdochium* in Arsk (but not Laishevo) (Table S7), and the relative abundance of some of these taxa affecting *Microdochium* both positively (*Novosphingobium* (in roots)) and negatively (*Cellvibrio*, *Devosia* (in roots); *Tetracladium*, *Sclerotinia*, *Acidovorax* (in DPS)) was higher in Arsk than in Laishevo (Table S3). Therefore, the likely reason that these taxa had less effect on *Microdochium* in Laishevo than in Arsk was that the conditions in Laishevo were less suitable for these taxa to thrive than those in Arsk. In contrast, a number of taxa were predicted to affect *Microdochium* in Laishevo (but not Arsk) (Table S7), and the relative abundance of some of these taxa affecting *Microdochium* both positively (*Itersonilia*, *Pedobacter* (in DPS)) and negatively (*Actinoplanes*, *Alpinaria*, *Typhula*, *Opitutus*, *Mesorhizobium*, *Nectria*, *Bradyrhizobium*, *Clohesyomyces*, *Kineosporia*, *Chaetomium* (in roots); *Phaeosphaeria*, *Helgardiomyces*, *Typhula* (in DPS)) was higher in Laishevo than in Arsk (Table S3). Therefore, it can be presumed that these taxa have the potential to affect *Microdochium*, but the conditions of Arsk agrocenosis were not suitable enough to provide the sufficient growth of these taxa required for affecting *Microdochium*. A number of taxa were predicted to affect *Microdochium* only within the dataset from which wheat samples were excluded (Table S7), and the relative abundance of some of these taxa affecting *Microdochium* both positively (*Caulobacter*, *Herbaspirillum*, *Massilia*, *Phenylobacterium*, *Sphingomonas* (in roots)) and negatively (*Acidovorax* (in DPS)) was lower in wheat compared to either rye, or triticale, or both crops (Table S3). Therefore, the likely reason that these taxa affected *Microdochium* in rye and triticale but not in wheat was that the abundance of these taxa in wheat did not reach the level required for affecting *Microdochium*.

Several taxa had the most significant effect on *Microdochium* within all four or three of the four datasets (Table 4). These taxa were accepted as those that cause the most reproducible effect (that was not dependent (or weakly dependent) on the types of crops and agrocenoses) on *Microdochium* and thus as the main candidates that prevent or, contrarily, stimulate the development of this snow mold fungus.

Four bacterial genera (*Cryobacterium*, *Rhizorhabdus*, *Chryseobacterium*, and *Rhodococcus*) were among the top candidates to have a positive effect on *Microdochium*. Thus, the high abundance of these bacteria within winter crop-associated communities may serve as a marker for the risk of snow mold development. The *Cryobacterium*

genus includes psychrotolerant bacteria [53–55]. *Rhizorhabdus* species inhabit soil and the rhizosphere and have been shown to destruct xenobiotics, herbicides, and antibiotics [56–60]. *Chryseobacterium* species have been previously found in the rhizosphere and endosphere of wheat [61–63]. *Rhodococcus* species are widespread in the endosphere of different plant species, including cereals, and can exert plant growth-promoting, disease-restraining, and fungicidal effects [64–69]. However, in our study, we revealed a positive correlation between *Rhodococcus* and *Microdochium* abundance, indicating that bacteria of the *Rhodococcus* genus have a rather positive effect than negative effect on the snow mold causal agent. At the same time, the *Rhodococcus* genus contains at least one phytopathogenic species, *R. fascians* [64, 65, 69], which can be presumed to cooperate with other phytopathogens, particularly *Microdochium*, during plant colonization.

Three bacterial genera (*Cellulomonas*, *Lechevalieria*, and *Pseudoxanthomonas*) and six fungal genera (*Leptosphaeria*, *Neoascochyta*, *Cladosporium*, *Entimomentora*, *Pseudogymnoascus*, and *Cistella*) were among the top candidates to have a negative effect on *Microdochium*. *Cellulomonas* and *Lechevalieria* (syn. *Lentzea*), both belonging to actinomycetes, have been previously found in the wheat rhizosphere [70, 71]. For the members of both of these genera, plant growth-promoting effects have been shown [72, 73], whereas their phytopathogen-restricting activities have only been suggested based on genome analyses [71, 74] but have not been experimentally demonstrated. Gram-negative bacteria of the *Pseudoxanthomonas* genus have been revealed among plant endophytes [75–77], but the phytopathogen-restricting activity of these bacteria has not been assessed so far.

Among the six fungal genera predicted in our study to have a negative effect on *Microdochium*, three genera (*Leptosphaeria*, *Neoascochyta*, *Cladosporium*) include phytopathogenic fungi. *Leptosphaeria* (*Ph. sclerotioides*), a little-known snow mold causal agent [41, 78], and *Microdochium*, a well-known snow mold causal agent, according to our results, seem to compete for the ecological niche within plant roots. Representatives of the *Neoascochyta* genus inhabit various niches, including cold arctic soils [79, 80], and some species of this genus (*N. europaea* and *N. graminicola*) cause wheat diseases [81].

Within the *Cladosporium* genus, phytopathogens that cause various plant diseases have been described [82–86], including those that synthesize mycotoxins [87]. Herewith, this species also includes plant-beneficial fungi [88–94]. Particularly, *Cladosporium* fungi constitute up to 80% of the endophyte seed community in wheat [95]. *Cladosporium* fungi have also been shown to suppress the growth of phytopathogenic fungi, and some *Cladosporium* species (*C. cladosporioides* and *C. oxysporum*) even parasitize causal agents of powdery mildew (*Blumeria graminis*) and rust (*Puccinia striiformis f. cn. tritici*, *Melampsora medusae f. sp. deltoidae*) [96–98]. Therefore, when considering the use of *Cladosporium* fungi as protective agents against snow mold, it is crucial to conduct thorough testing of *Cladosporium* strains, as this genus includes not only beneficial species but also phytopathogenic ones, some of which can produce mycotoxins.

Among the *Entimomentora*, *Cistella*, and *Pseudogymnoascus* genera, phytopathogens have not been described. Within the *Entimomentora* genus, the only almost uncharacterized species, *E. hyalina*, has been isolated from wheat field soil [99]. Representatives of the *Cistella* genus form mycorrhiza with *Ericaceae* plants [100] and have also been detected in *Cyperaceae* and *Caryophyllaceae* plants and in winter rye after wintering [21, 101, 102]. The *Pseudogymnoascus* genus includes fungi that inhabit various niches and possess psychrophilic/psychrotolerant properties [103–107]. *Pseudogymnoascus* fungi have also been revealed in the cereal endosphere [108]. Some representatives of this genus have been shown to synthesize fungicidal compounds that inhibit the growth of phytopathogens [52, 104, 109–111]. Due to these properties of *Pseudogymnoascus* fungi and because their abundance has a high and representative negative weight correlation with *Microdochium* abundance, the *Pseudogymnoascus* genus seems to lead the list of candidates for biological agents against snow mold.

Thus, our study highlights key candidates from a diverse array of plant-associated microorganisms for isolation and testing of their protective properties against *Microdochium*-induced snow mold disease. Certainly, the expected protective properties of these candidates must be validated through a series of laboratory and field tests before these microorganisms can be recommended for agricultural use. The contribution of our study is that it significantly narrows the scope of the search for microorganisms that may potentially suppress snow mold, thereby enhancing the efficiency of selecting those with desirable properties. Demonstratively, we identified 448 and 259 microbial genera within the root and DPS samples, respectively, but testing numerous representatives from all these genera in laboratory and field experiments is not feasible due to the extensive experimental workload involved. In turn, based on our investigation, we propose a focused list of genera where strains with the desired property are most likely to be found. The targeted isolation of the proposed microorganisms, followed by their thorough testing, will facilitate the selection of the most effective strains for enhancing snow mold management.

Conclusions

The variability of bacterial microbiomes in winter cereal crops (rye, wheat, and triticale) is primarily determined by crop growth conditions, whereas crop species contribute more to the variability of fungal communities. The mycobiome composition in rye and wheat, including the snow mold pathocomplex, exhibits a high degree of variability, whereas the triticale mycobiomes can show considerable similarity to either rye or wheat mycobiomes, depending on the particular agrocenosis. In rye, *Microdochium* strongly dominates over other snow mold fungi, whereas the snow mold pathocomplex in wheat is composed of various fungi, including *Ph. sclerotioides*, which, only in wheat, can dominate over other snow mold fungi under particular conditions.

Bacteria of the *Cryobacterium*, *Rhizorhabdus*, *Chryseobacterium*, and *Rhodococcus* genera are candidates to have a positive effect on *Microdochium*, and thus, their high abundance within winter crop-associated microbial communities may serve as a marker for the risk of *Microdochium*-induced snow mold development.

Bacteria of the *Cellulomonas*, *Lechevalieria*, and *Pseudoxanthomonas* genera and fungi of *Cladosporium*, *Entimomentora*, *Pseudogymnoascus*, and *Cistella* genera are top candidates to have a negative effect on *Microdochium*, and thus, the representatives of these genera are prime candidates for testing their plant-protective properties against *Microdochium*-induced snow mold disease and further use in agricultural practice.

Abbreviations

ASV	Amplicon sequence variant
CSS	Cumulative sum scaling
DPS	Dead parts of shoots
FHB	Fusarium head blight
FWD	Fusarium wilt disease
Log2FC	Logarithm of fold change
PCA	Principal component analysis
PCoA	Principal coordinate analysis
SRA	Sequence reading archive
W_Log2FC	The weighted logarithm of fold change

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

Supplementary Material 4

Supplementary Material 5

Supplementary Material 6

Supplementary Material 7

Supplementary Material 8

Supplementary Material 9

Supplementary Material 10

Author contributions

IS, MP, VG conceived and designed the study. IC, ER, OG performed the experiments. IS, AB, SP, MP performed bioinformatics and statistical analysis. VK contributed to the design of the study and critically reviewed the manuscript. IS and VG wrote the manuscript with contributions from all the other authors. All authors have read, revised, and approved the final manuscript.

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Data availability

All data used in this study are present in the main text and supplementary materials. Sequencing data from this study can be found in National Center for Biotechnology Information (NCBI) Sequence Reading Archive (SRA) under the PRJNA1154949 bioproject. Information on the ASV sequences, abundance of ASVs in the analyzed samples, taxonomic annotations of ASVs, and sample sheets describing sample nomenclature are presented on GitHub (https://github.com/ildar-ITS/16S_ITS2_Wheat_Triticale_Rye_DPS_Roots_Microbiome).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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