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Fungal community change in selected fluvisols under simulated flooding condition

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Abstract. The soil mycobiome is an important part of the numerous biogeochemical processes taking place in the soil. Its activity and diversity are influenced by many factors, including soil moisture. In this study, the effect of a 14-day simulated flood on the mycobiome of three different Fluvisols in microcosm experiment was assessed using next-generation sequencing. The results obtained showed that excessive moisture alters the structure of the mycobiome and the amounts of pathogenic, parasitic, and endophytic fungi. Among others, an increase in the occurrence of saprotrophic fungi of the genera *Trichoderma*, *Talaromyces*, and *Schizothecium* was noted. At the same time, the study showed a decrease in the abundance of arbuscular mycorrhizal fungi from the phylum *Glomeromycota* and *Mucoromycota* as a result of flooding. In addition, the structure of the soil mycobiome has been shown to be closely related to soil type – statistically significant correlations of individual fungal genera with the clay and silt or sand content of the soil were obtained. Future research on the soil mycobiome under flooding conditions may help to understand changes in soil biogeochemical processes following flooding, the occurrence of which is increasing with climate change.

Keywords: flood, fluvisols, fungi, microcosm experiment, mycobiome, soil moisture

INTRODUCTION

Fungi are an important part of the soil biomass (Ritz, Young, 2004) and their biodiversity is increasingly recognized as beneficial for soil quality (Duniere et al., 2017). The community of fungi in a particular ecosystem is called the mycobiome (Pagano et al., 2017; Yang et al., 2019). They are responsible for nutrient cycling, decomposition of organic matter, and mediate the formation of soil structure (Helfrich et al., 2015). The soil mycobiome provides important services relating to water dynamics, nutrient cycling and disease control. They are also important as decomposers. They convert hard-to-digest organic matter into forms that are accessible to other organisms (Lee Taylor, Sinsabaugh, 2015). Fungal diversity and the complexity of mycobiome structure have a positive effect on the rate of nutrient decomposition (Hiscox et al., 2015). Fungi also form symbiotic associations with plants, which has a further impact on the assimilation of nutrients (Yang et al., 2017).

Fungi are affected by climate, land use intensity, and soil parameters such as temperature, pH, and mineral availability (Jamiołkowska et al., 2018; Oehl et al., 2017). Many authors report that soil fungi depend on soil moisture (Frąc et al., 2018), but there is a lack of specific data in this area. Using the Scopus database, the keyword 'fungi floodplains' yields 153 papers; and for the keyword 'fungi in soil under flood' only 48 papers. Many papers relate to peat or wetland soils and rice cultivation (Dong et al., 2023; Zhai et al., 2020). It is known, that fungi require more water for growth than bacteria (Furtak, Gałązka, 2019) and normally occur in well aerated soil layers. The most fungi and yeasts can grow at $a_w < 0.80$ (water activity) (Kunicki-Golfinger, 2008) and the optimal moisture content for fungi is 60% of soil water capacity (Borowik, Wyszkowska, 2016). Soil fungal community analysis at the Yellow River Floodplain Ecosystems Research Station showed that the soil was dominated by fungi from the phyla *Ascomycota, Mortierellomycota, Basidiomycota* and *Glomeromycota*. Researchers analyzed also the soil mycobiome in summer and autumn, and showed that the abundance of individual taxa varies significantly between these seasons. Unfortunately, in the literature is little research determining how excessive moisture, soil overwatering, and floods affects soil fungi. A study by Wagner et al. (2015) found that as a result of oxygen depletion under flooding condition the number of fungi decreases. Studies of Liao et al. (2018) indicated that flooded paddy soils have a lower biomass of microorganisms, including fungal markers, compared to

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unflooded soils. The authors noted a decrease in soil fungal PLFA (phospholipid fatty acid) ranging from 4.17 to even 55.6% between unflooded and flooded variants. Unfortunately, the taxonomic structure of the microbiome and mycobiome was not analyzed.

The largest number of studies about impact of flooding on mycobiome relate to the arbuscular mycorrhizal fungi (AMF), which are an important component of the soil microbiome, forming an obligate symbiosis with 70–80% of plant species worldwide (Heijden et al., 2015). Their role in the soil environment is not only to promote plant growth (Cozzolino et al., 2016), but also to form soil aggregates which prevents soil erosion (Rillig et al., 2015) and protect plants from pathogen infection (Ronsheim, 2016). Some studies have shown that agricultural soils showed higher AMF diversity compared to soils from natural habitats (Al-Yahya'ei et al., 2011). In the context of flooded areas and rice cultivation, the researchers showed that AMFs participate in the exchange of C and P with rice under flooded conditions, and also increased rice plant biomass and grain yield (Bao et al., 2019; Wang et al., 2021).

Based on the sparse literature data, we know that the soil mycobiome changes as a result of flooding, and the overall fungal biomass decreases. However, there is a lack of information about the impact of floods on the soil mycobiome structure and changes of taxa distribution. The progressive climate change is associated with the occurrence of phenomena such flood, and their impact on soil microorganisms is of importance for agriculture and food security (Furtak, Wolińska, 2023). Understanding the changes that occur in the soil environment as a result of flooding can help in the future development of methods to regenerate the soil after such events. For this purpose, we have undertaken the determination of structural diversity of fungal community under simulated flood condition using NGS (Next Generation Sequencing) methods.

MATERIALS AND METHODS

Soil samples and microcosm experiment

Based on a soil and agricultural map on the scale of 1:25000 three soils which are classified as fluvial soils (Anjos et al., 2014) were selected. The selected sites were grasslands, with grasses dominating, and wild garlic and field horsetail present. There was little vegetation at location F3. The agricultural map provided preliminary information on the particle size distribution of these soils and sampling sites were pre-selected on this basis. In addition, the analysis of the granulometric composition confirmed the structural differentiation of the selected soils, which were classified as: sandy loam – F1 and F2, and sand – F3 (Table 1). The soils differed not only in their granulometric composition, but also in the content of total carbon, organic carbon, total nitrogen, and organic matter. The results made it possible to classify the selected soils according to their fertility as follows: F1 > F2 > F3; see Furtak et al. (2019) for details.

Soil samples (three per each Fluvisols) were collected as sods (30 × 30 × 25 cm) with live vegetation and then placed in a separate transparent, polypropylene container (33 × 33 × 42 cm), and flooded with water from the river in a volume of about 12 L per container (Vistula River, Janowiec, Lubelskie voivodeship; 51°19'06.8" N 21°54'53.5" E). Samples were taken twice: fresh soils before flooding and after 14 days of water stagnation. Samples were taken through 10 small random punctures (0–20 cm depth) in each container, then soil was pooled for each Fluvisols.

Other soil parameters – pH and enzymatic activity – were also determined, as described in the paper (Furtak et al., 2020).

DNA extraction and next generation sequencing (NGS)

Total DNA was extracted from each fluvisols sample using the FastDNA™ SPIN Kit for Soil (MPBiomedical) according to the manufacturer's instructions.

Next generation sequencing was performed at Genomed S.A. (Warsaw, Poland). Sequencing was performed on the MiSeq Illumina Inc. system in 2 bp × 250 bp paired-end technology. Amplification of the ITS1 hypervariable region was performed with Q5 Hot Start High-Fidelity 2x Master Mix according to the manufacturer's instructions using ITS1Fl2 (5'-GAACCWGCGGARGGATCA-3') and 5.8S (5'-CGCTGCGTTCTTCATCG-3') primers (Schmidt et al., 2013).

Amplicon sequence variants (ASVs) were resolved using the DADA2 version 1.8 package (Callahan et al., 2016) in R version 3.5.1 (Team, 2016). Based on the se-

Table 1. Soils used in the experiment (see also Furtak et al., 2020).

Abbreviation	Location	GPS coordinates	Soil texture, mm [%]			Textural classes acc. to the USDA classification	pH_{H2O}
			2.0–0.05	0.05–0.002	<0.002		
F1	Wojszyn, Puławy County	51°20'03.4"N 21°56'43.2"E	58	38	4	sandy loam	7.50
F2	Janowiec (1), Puławy County	51°19'29.9"N 21°55'19.2"E	67	30	3	sandy loam	7.67
F3	Janowiec (2), Puławy County	51°19'14.4"N 21°54'42.9"E	92	8	0	sand	7.53

quence quality plots, both forward and reverse reads were trimmed respectively to 250 bp and primers sequences were removed from all reads. The following filtering parameters were used: maxN = 0, maxEE = 2 and trunc Q = 2. Other parameters were set to default. The error rates were estimated by learnErrors using one million reads. Sequences were dereplicated using derepFastq with default parameters and exact sequence variants were resolved using DADA2. Next, removeBimeraDenovo was used to remove chimeric sequences. From quality-filtered reads ITS1 regions were extracted using the latest version (1.1.2) of ITSx software (Bengtsson-Palme et al., 2013). Taxonomy was assigned against the latest version of the UNITE database (Tedersoo et al., 2018) using idTAXA classifier (Murali et al., 2018). The resulting taxonomy and read-count tables constructed in DADA2 were appropriately converted and imported into the *phyloseq* (1.22.3) package (McMurdie & Holmes, 2013). All sequences are available at the NCBI database under the bioproject accession number: PRJNA552453 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA552453/).

Statistical analysis

Statistical analyses were performed using Statistica ver. 10.0 (StatSoft. Inc., Tulsa, OK, USA). Diagrams were generated using MS Excel software (Microsoft Corporation, 2016). The results were also subjected to principal component analysis (PCA) in order to determine the common relationships between soil parameters and the mycobiome (Statistica ver. 10.0 StatSoft. Inc., Tulsa, OK, USA). Indices (Shannon, Simpson, Evenness) were calculated using the estimate_richness function implemented in the *phyloseq* package. Venn diagrams were generated from the NGS results (at the genus level) using version 3.7.2 of the Cytoscape software (Shannon et al., 2003).

RESULTS

A decrease in diversity indices and the number of identified genera after 14 days of stagnant water was noted in all Fluvisols (Table 2).

Representatives of *Basidiomycota* were the most abundant (33.67–67.23%) in all soils, and their presence increased as a result of flooding in all Fluvisols (Figure 1). The second most abundant phyla were *Ascomycota* (25.87–56.62%), which abundance decreased as a result of inundation in all samples. Relative abundance of *Chytridiomycota* decreased in F1 and F2, when increased in F3. Phylum *Blastocladiomycota* occurred only in F3_C (0.34%) and F2_C (0.06%). Representatives of *Entomophthoromycota* was present only in F1_F (0.24%). *Entorrhizomycota* was absent in F3 and *Glomeromycota* in F2. Relative abundance of *Mucoromycota* decreased in F1 and increased in F2 and F3.

In all Fluvisols 30 fungal genera were present in both variants of the experiment (Figure 2C), with the genera *Coniochaeta* and *Acremonium* being the most abundant in the fresh soils, while after 14 days of flooding, fungi of the genus *Pholiotina* and *Hemimycena* were dominant (Figure 3 and Table 3). However, these are averaged data. Analyzing the individual soils separately (Table 3 and Figure 4), it is noticeable that fungi from *Acremonium* (16.69%) were dominant in F1_C and *Hemimycena* (20.11%) in F1_F. In the F2 in the control, the genus *Coniochaeta* was dominant (12.31%) and in the flooded it was *Pholiotina* (41.02%). In the F3, the genus *Coniochaeta* (11.33%) was dominant before flooding and *Paranamyces* (8.51%) after flooding. These genera can be considered the core mycobiome, *i.e.* the group of microorganisms present in the Fluvisols regardless of soil type, pH, parameters and effect of stress.

The analysis of the diversity of fungal genera (Figure 3 and 4) showed that *Pholiotina* was the dominant genus (average 8.46%), but its representatives were most abundant in F2_F (41.02%), while it was almost absent in F3 (C – 0.20%, F – 0.00%). Fungi from the genera *Hemimycena* and *Acremonium* occurred with an average relative abundance 6.59%, and 6.14% respectively, and were the most abundant in F1. It is also worth noting that fungi from the genus *Chaetosphaeronema* were only present in F1 (5.44–5.22); while representatives of *Melanconium* was completely absent in F3.

Table 2. Fungal diversity indexes (at genera level).

Fluvisols	Symbol	Experiment stage	Number of identified genera	Shannon (H')	Simpson (1-D)	Evenness (E)
F1	F1_C	Fresh soil (control)	86	3.607	0.948	0.429
	F1_F	14 days after flooding	74 ↓	3.087 ↓	0.916 ↓	0.296 ↓
F2	F2_C	Fresh soil (control)	95	3.764	0.960	0.454
	F2_F	14 days after flooding	78 ↓	2.782 ↓	0.814 ↓	0.207 ↓
F3	F3_C	Fresh soil (control)	99	3.800	0.961	0.451
	F3_F	14 days after flooding	78 ↓	3.611 ↓	0.959 ↓	0.474 ↑

↑ increase of value compared to control; ↓ decrease of value compared to control

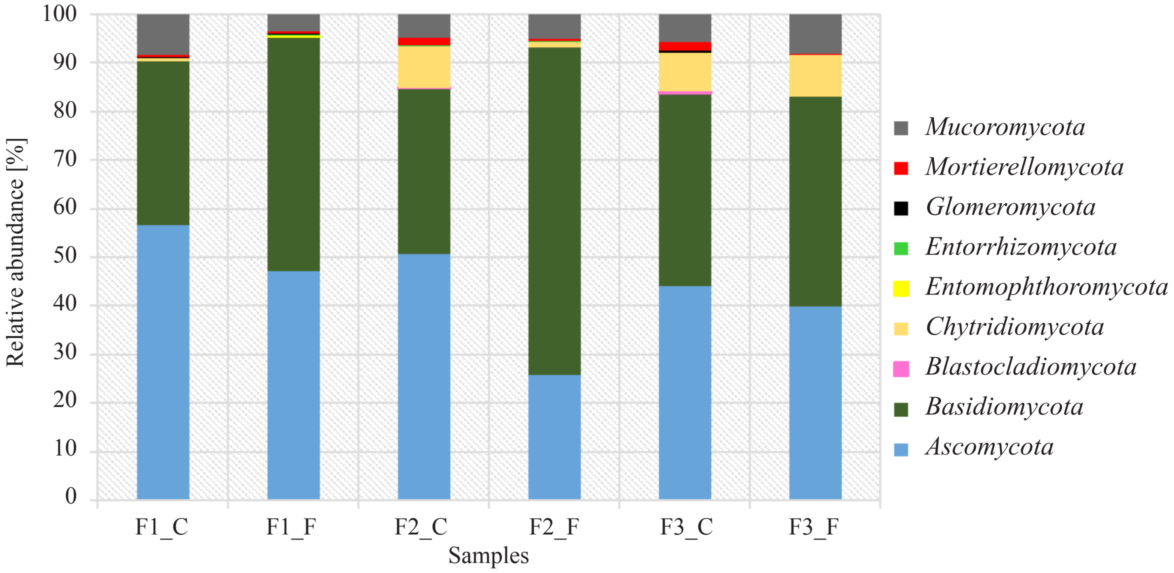


Figure 1. Impact of flooding on relative abundance (%) of fungal phyla in selected Fluvisols (soil symbol notations can be found in Table 2).

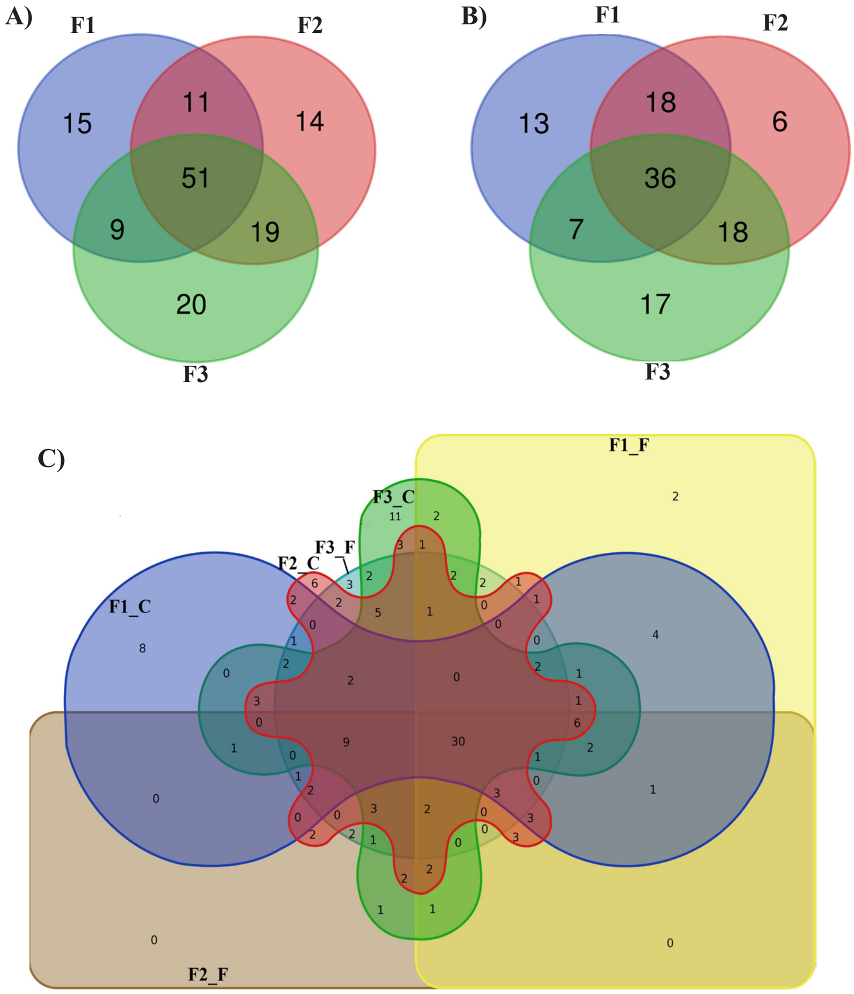


Figure 2. Venn diagrams based on fungal genera: A) Fresh (control) soils; B) Soils after 14 days of flooding; C) Control soils and soils after 14 days of flooding (soil symbol notations can be found in Table 2).

Table 3. Change in relative abundance [%] of the 5 most abundant fungal genera under flooded conditions.

Soil sample	Genera				
	Pholiotina	*Hemimycena*	*Acremonium*	*Coniochaeta*	*Mucor*
F1_C	1.58	0.97	16.69	1.23	6.77
F1_F	5.13 ↑	20.11 ↑	14.02 ↓	0.60 ↓	2.90 ↓
F2_C	2.83	3.94	3.90	12.31	4.04
F2_F	41.02 ↑	9.26 ↑	0.72 ↓	0.50 ↓	4.32 ↑
F3_C	0.20	2.18	0.74	11.33	4.29
F3_F	0.00 ↓	3.09 ↑	0.79 ↑	7.43 ↓	4.67 ↑

↑ increase of value compared to control; ↓ decrease of value compared to control; soil symbol notations can be found in Table 2

Table 4. The relative abundance [%] of selected potential pathogenic fungi in examined soils.

Genera	Soil samples					
	F1_C	F1_F	F2_C	F2_F	F3_C	F3_F
Alternaria	0.40	0.37	0.06	0.51	1.17	0.08
Amylostereum	0.13	0	0.22	0	0	0
Arthrinium	0	0.08	0	0	0	0
Aspergillus	0.24	0.22	1.63	0.34	2.71	3.49
Cadophora	0.17	0.45	0.04	0.35	0.28	0
Candida	1.04	0	3.92	1.74	2.54	2.17
Entyloma	0.43	0	0.41	0	0.32	0
Fusarium	0.82	0	0.76	0.70	0	0.93
Metarhizium	2.46	8.47	0.86	2.03	0.25	0.75
Rhizoctonia	0.31	0	0.27	0	0.19	0

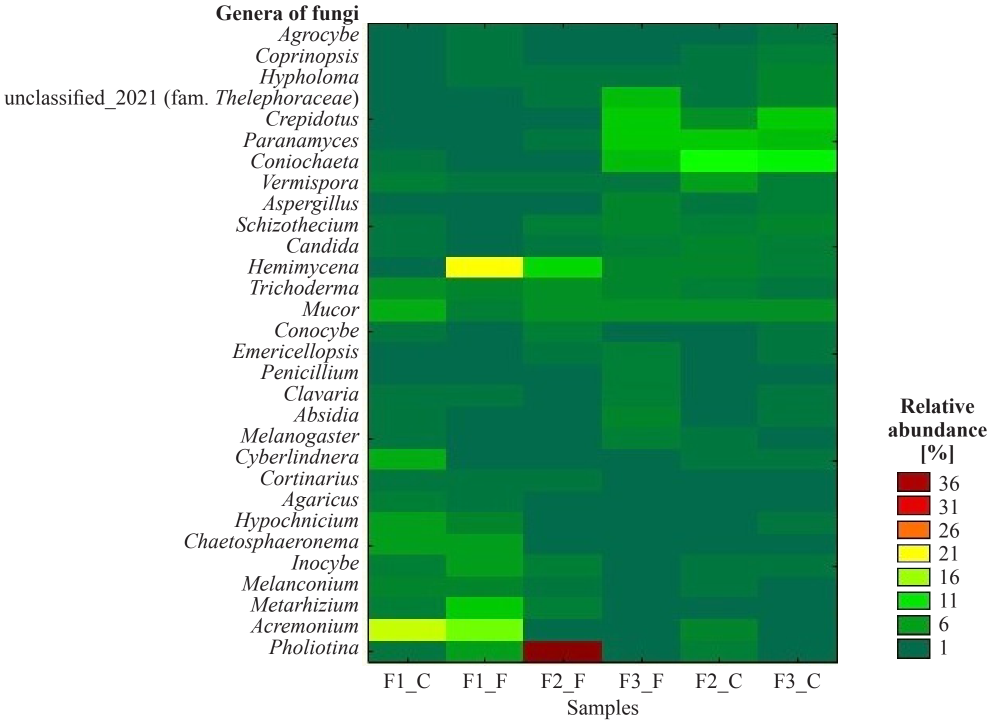


Figure 3. Top genera – with mean relative abundance ≥1% in all samples ($n = 6$); soil symbol notations can be found in Table 2.

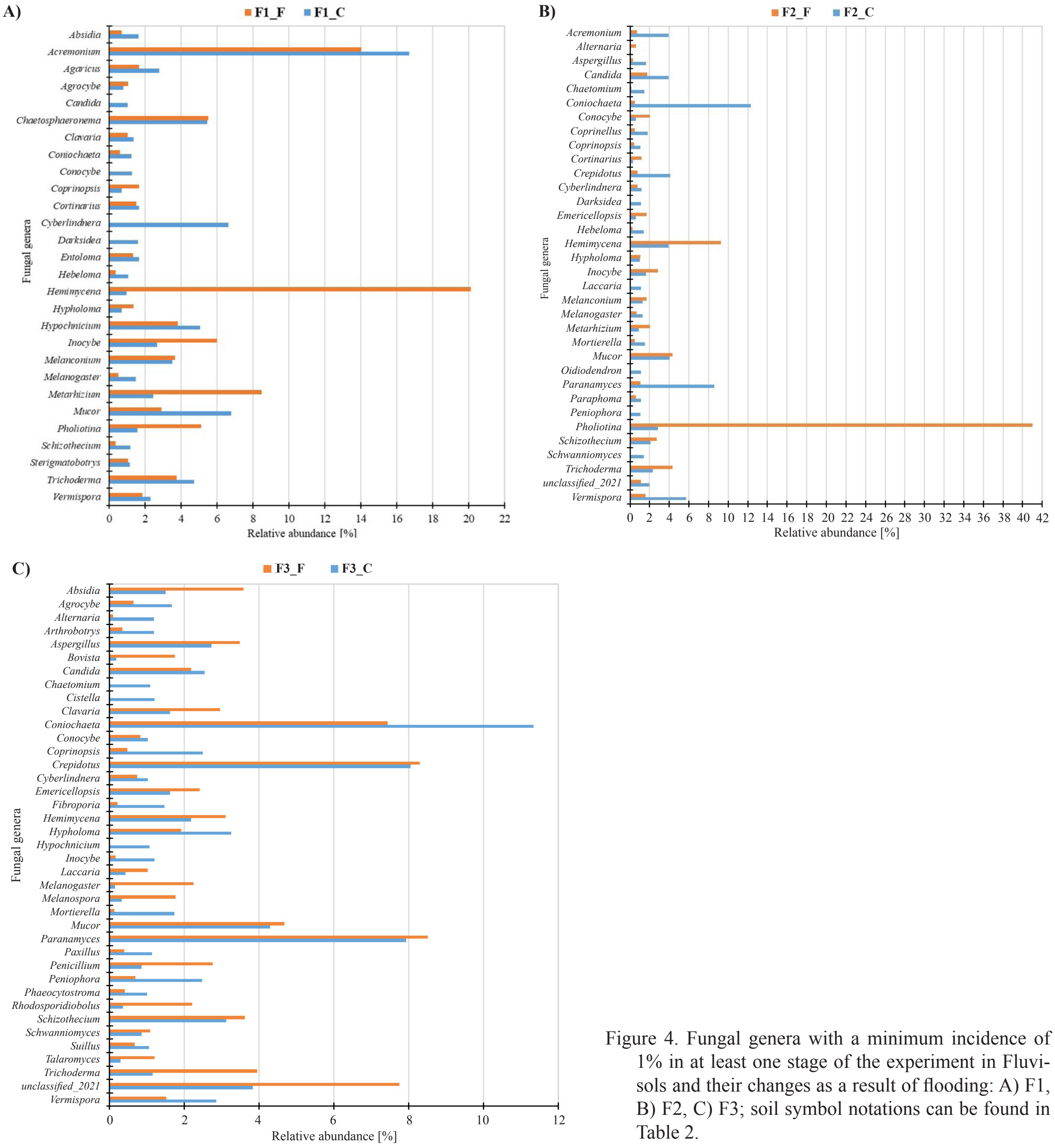
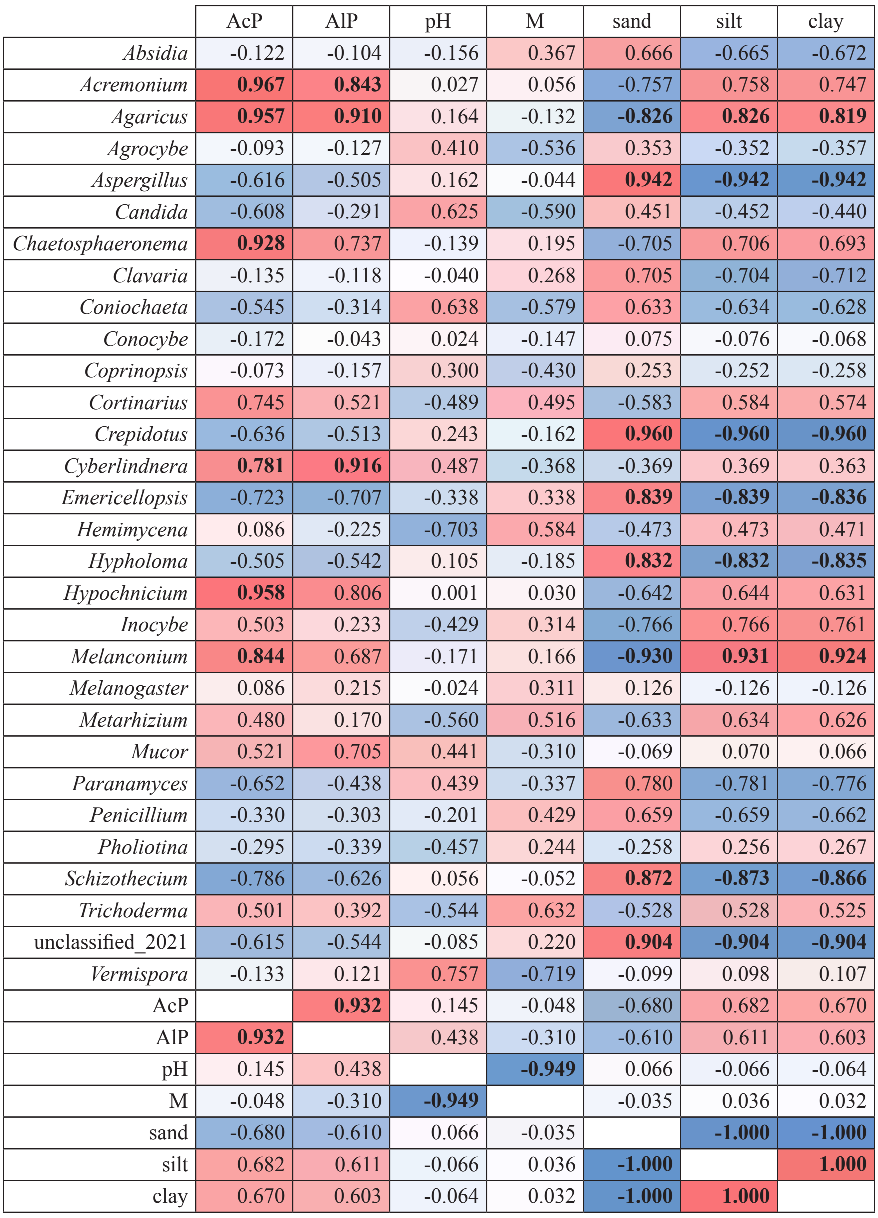


Figure 4. Fungal genera with a minimum incidence of 1% in at least one stage of the experiment in Fluvisols and their changes as a result of flooding: A) F1, B) F2, C) F3; soil symbol notations can be found in Table 2.

It should be noted that the fungal abundance was also dependent on the type of the soils. For example, the relative abundance of the genera *Inocybe* and *Hypholoma* increased as a result of 14 days of inundation in F2, but decreased in F3 (Figure 4A-C). The relative abundance of the genus *Trichoderma* decreased as a result of inundation in F1 but increased in F2 and F3. As a result of flooding, the presence of *Darksidea* spp., *Cyberlindnera* spp., and *Candida* spp. completely disappeared in F1 (Figure 4A). In F2, flooding resulted in the disappearance of fungi from the genera *Darksidea, Oidiodendron, Peniophora*, and *Schwanniomyces* (Figure 4B). In F3 the representatives of *Chaetomium*, *Cistella*, and *Hypochnicium* disappeared (Figure 4C). Another interesting observation is that fungi of the genus *Chaetosphaeronema* were only present in the F1, in both variants of the experiment with 5.44–5.52% relative abundance (Figure 4A). These results indicate that the habitat itself also influences the behavior of fungal mi-



	AcP	AlP	pH	M	sand	silt	clay
Absidia	-0.122	-0.104	-0.156	0.367	0.666	-0.665	-0.672
Acremonium	**0.967**	**0.843**	0.027	0.056	-0.757	0.758	0.747
Agaricus	**0.957**	**0.910**	0.164	-0.132	**-0.826**	**0.826**	**0.819**
Agrocybe	-0.093	-0.127	0.410	-0.536	0.353	-0.352	-0.357
Aspergillus	-0.616	-0.505	0.162	-0.044	**0.942**	**-0.942**	**-0.942**
Candida	-0.608	-0.291	0.625	-0.590	0.451	-0.452	-0.440
Chaetosphaeronema	**0.928**	0.737	-0.139	0.195	-0.705	0.706	0.693
Clavaria	-0.135	-0.118	-0.040	0.268	0.705	-0.704	-0.712
Coniochaeta	-0.545	-0.314	0.638	-0.579	0.633	-0.634	-0.628
Conocybe	-0.172	-0.043	0.024	-0.147	0.075	-0.076	-0.068
Coprinopsis	-0.073	-0.157	0.300	-0.430	0.253	-0.252	-0.258
Cortinarius	0.745	0.521	-0.489	0.495	-0.583	0.584	0.574
Crepidotus	-0.636	-0.513	0.243	-0.162	**0.960**	**-0.960**	**-0.960**
Cyberlindnera	**0.781**	**0.916**	0.487	-0.368	-0.369	0.369	0.363
Emericellopsis	-0.723	-0.707	-0.338	0.338	**0.839**	**-0.839**	**-0.836**
Hemimycena	0.086	-0.225	-0.703	0.584	-0.473	0.473	0.471
Hypholoma	-0.505	-0.542	0.105	-0.185	**0.832**	**-0.832**	**-0.835**
Hypochnicium	**0.958**	0.806	0.001	0.030	-0.642	0.644	0.631
Inocybe	0.503	0.233	-0.429	0.314	-0.766	0.766	0.761
Melanconium	**0.844**	0.687	-0.171	0.166	**-0.930**	**0.931**	**0.924**
Melanogaster	0.086	0.215	-0.024	0.311	0.126	-0.126	-0.126
Metarhizium	0.480	0.170	-0.560	0.516	-0.633	0.634	0.626
Mucor	0.521	0.705	0.441	-0.310	-0.069	0.070	0.066
Paranamyces	-0.652	-0.438	0.439	-0.337	0.780	-0.781	-0.776
Penicillium	-0.330	-0.303	-0.201	0.429	0.659	-0.659	-0.662
Pholiotina	-0.295	-0.339	-0.457	0.244	-0.258	0.256	0.267
Schizothecium	-0.786	-0.626	0.056	-0.052	**0.872**	**-0.873**	**-0.866**
Trichoderma	0.501	0.392	-0.544	0.632	-0.528	0.528	0.525
unclassified_2021	-0.615	-0.544	-0.085	0.220	**0.904**	**-0.904**	**-0.904**
Vermispora	-0.133	0.121	0.757	-0.719	-0.099	0.098	0.107
AcP		**0.932**	0.145	-0.048	-0.680	0.682	0.670
AlP	**0.932**		0.438	-0.310	-0.610	0.611	0.603
pH	0.145	0.438		**-0.949**	0.066	-0.066	-0.064
M	-0.048	-0.310	**-0.949**		-0.035	0.036	0.032
sand	-0.680	-0.610	0.066	-0.035		**-1.000**	**-1.000**
silt	0.682	0.611	-0.066	0.036	**-1.000**		**1.000**
clay	0.670	0.603	-0.064	0.032	**-1.000**	**1.000**	

Figure 5. Correlations between top fungal genera relative abundance and granulometric composition (% content of sand, silt, and clay fractions), moisture content (M), pH, acid phosphatase (AcP) and alkaline phosphatase (AlP) activities in the examined soils. The bolded values are statistically significant at $P < 0.05$ ($n = 6$).

croorganisms in addition to the impact of external conditions – in this case flooding.

Analysing the occurrence of potential pathogens in the soils studied (Table 4), it can be seen that their occurrence depended on the soil. In control F1 and F2 there were generally more such fungi present than in F3. As a result of flooding, the relative abundance of some potential pathogenic genera decreased, e.g. *Alternaria, Amylostereum, Entyloma*.

However, the relative abundance of representatives of *Fusarium* sp. and *Metarhizium* sp. increased markedly in all the investigated soils as a result of flooding. An interesting observation is also the increase in the occurrence of *Aspergillus* in F3 after flooding, when in F1 and F2 its relative abundance decreased.

There was a positive correlation (Figure 5) between AcP and AlP activity and the presence of fungi from the genera: *Acremonium*, *Agaricus, Chaetosphaeronema*, *Cyberlindnera*, *Hypochnicium,* and *Melanconium*. The realative abundance of the genera *Crepidotus*, unclassified_2021, *Schizothecium*, *Hypholoma*, *Aspergillus*, and *Emericellopsis* correlated positively with the content (%)

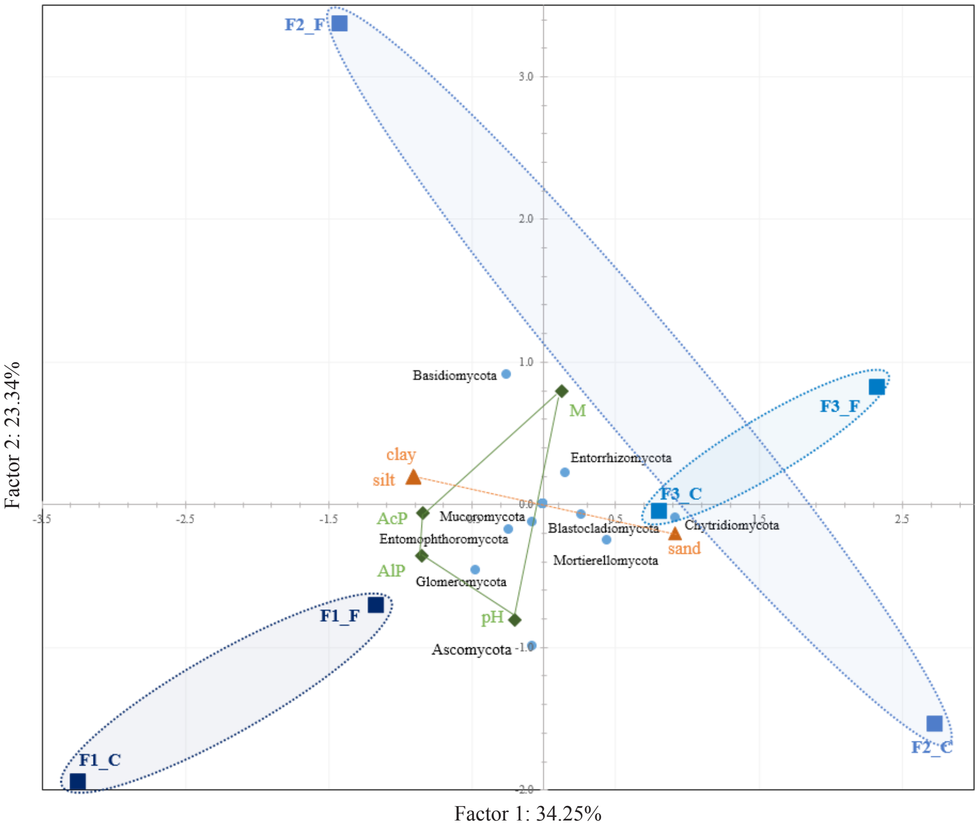


Figure 6. Principal component analysis (PCA) between acid phosphatase (AcP), alkaline phosphatase (AlP) activities, pH values, moisture (M) content, granulometric composition, fungal phyla relative abundance, and soil samples in different experimental stage; soil symbol notations can be found in Table 2.

of sand in soil, and negatively with the content of silt and clay in soils. In contrast, the relative abundance of fungi from *Melanconium* and *Agaricus* genera correlated negatively with sand content and positively with silt and clay content. Interestingly, the soil pH and moisture had no such significant effect on fungal occurrence as did granulometric composition.

PCA analysis with fungal phyla (Figure 6) showed that samples from F1 correlates positively in both phases of the experiment. In contrast, F2 correlates negatively in the flooding and control phases. In the case of F3, there was no correlation between the variants. *Basidiomycota* occurrence correlates positively with clay and silt content in the soil. In contrast, sand content correlates positively with the occurrence of phyla *Blastocladiomycota*, *Chytridiomycota,* and *Mortierellomycota*. Interestingly, soil moisture levels correlated positively only with phyla *Entorrhizomycota*, and negatively with *Ascomycota, Entomophthoromycota, Glomeromycota,* and *Mucoromycota*. The abundance of fungi from the *Ascomycota* phylum strongly correlated with pH, AcP, and AlP, as did the presence of *Entomophthoromycota, Glomeromycota*, and *Mucoromycota*. The presence of *Basidiomycota* was correlated with F2_F, where it was most abundant.

DISCUSSION

It is generally accepted that excessive moisture primarily affects Gram-negative bacterial and fungal communities, which are normally found in well-aerated soil layers where flooding begins to lack oxygen (Unger et al., 2009; Wagner et al., 2015). The sensitivity of fungi to the oxygen content of the soil (Tonouchi, 2009) makes them likely to be indicators of flood stress in soils (Francioli et al., 2022). The results of the present study, confirm these reports, as a decrease in fungal relative abundance and diversity was recorded in soils subjected to flooding.

The distribution of fungi in floodplain environments is also related to vegetation characteristics, soil chemical parameters and soil use (Solís-Rodríguez et al., 2020). In the presented study, it was shown that the granulometric composition of soils influenced the composition of fungal communities and their response to flooding (Figure 5 and 6). Other researchers also found that perennial agriculture and coniferous forest soils had the highest fungal marker contribution, while rice fields and freshwater soils had the lowest contribution (Drenovsky et al., 2010). In different land use types, the share of fungal fatty acids differed by up to 8.4 times. Studies have shown that fungi decrease in soils with high water availability and are often favored by nutrient poor soils (Drenovsky et al., 2004; Millard, Singh, 2010). This is somewhat in line with the results of the present study, as the very light Fluvisols (F3), which was C- and N-poor showed the highest fungal diversity (Table 2). An additional factor influencing changes in the soil mycobiome under flood conditions is temperature. Sanchez-Rodriguez et al. (2019) showed that the percentage of putative arbuscular mycorrhiza and fungi (%) decreased with increasing temperature, but mainly due to a combination of flooding × higher temperatures (Sánchez-Rodríguez et al., 2019). Different temperature treatments were not used in this study, but this is a valuable indication for future research. Changes in soil pH are a commonly reported consequence of flooding (Furtak et al., 2020) and have been identified as a key factor affecting microbial structure in a wide range of soils and ecosystems (Bardelli et al., 2017; Guo et al., 2020). However, in the present study, pH value correlated negatively with soil moisture content (Figure 5 and 6), but there was no statistically significant correlation of pH with mycobiome community composition. A positive correlation has been shown between soil moisture and the occurrence of fungi from the phylum *Entorrhizomycota* (Figure 6), which is reasonable because there is a hypothesis that these fungi spread through soil moisture (Riess et al., 2019). Representatives of *Ascomycota* dominated in dry, fresh soils, which was also reflected by their negative correlation with soil moisture (Figure 6). In studies (Li et al., 2020) *Ascomycota* dominated both in dry land and paddy field, however, in flooded soils their numbers were significantly lower, and the numbers of *Basidiomycota*, *Mortierellomycota* and *Olpidiomycota* increased. This is an understandable relationship due to the aerobic metabolism of the *Ascomycota*. This confirms our research, where we also observed the dominance of *Basidiomycota* in flooded soils. It was reported that *Chytridiomycota* was the dominant fungus on dry land, with an abundance of 13.26%, and its abundance decreased to 0.1% in flooded fields (Li et al., 2020). In this study, a significate decrease in the number of this fungi was noted as a result of flooding in soil F1 and F2; and an increase in the abundance of *Chytridiomycota* representatives in F3. Moreover, the analysis showed that the presence of *Chytridiomycota* strongly positively correlates with the sand content of the soil (Figure 6). Fungi from this phylum are saprotrophs, and their zoospores are able to actively move in water (Volk, 2013). In addition, it is believed that these organisms mainly inhabit aquatic ecosystems, and some of them are plant pathogens, e.g. *Synchytrium endobioticum* (McConnaughey, 2014).

The largest number of studies on the mycorrhizal mycobiome in floodplains are concerned with mycorrhizal fungi. Arbuscular mycorrhizal fungi (AMF) are commonly present in wetlands, including rice fields (Bao et al., 2019). Among AMF, fungi from the *Glomeromycota* and *Mucoromycota* phyla are distinguished. In the present study, representatives of *Glomeromycota* were identified in F1 and F3, and their relative abundance decreased as a result of flooding (from 0.4 to 0.2 and from 0.4 to 0.04%, respectively) (Figure 1). *Lentamyces* (from *Mucoromycota* phylum) was recorded in F2 and disappeared as a result of flooding. A study by Unger et al. (2009) showed that the presence of mycorrhizal fungal markers in the soil decreased as a result of stagnant water (greenhouse conditions) (Unger et al., 2009). Sanchez-Rodriguez et al. (2019) reported under mesocosm conditions that soil flooding caused a decrease in the biomass of microorganisms, actinomycetes and arbuscular mycorrhiza. A study by Wang et al. (2010) showed that the intensity of AMF colonisation decreases along hydrological gradients, and a study by Wang et al. (2011) demonstrated that seawater inundation significantly alters the diversity and distribution patterns of AMF communities in the roots of three mangrove species (Wang et al., 2010, 2011). In contrast, Wang et al. (2016) found that high flooding intensity significantly reduced AMF diversity levels, while moderate flooding caused markedly different effects between the two species: it favoured AMF diversity in aquatic species, but inhibited those in semi-aquatic species (Wang et al., 2016). When Zheng et al. (2020) revealed that mycorrhizal fungi increased peach tolerance to flooding by inducing proline accumulation and improving root architecture.

Francioli et al. (2022) showed an increase in the abundance of pathogenic fungi and saprophytes in flooded soil under wheat cultivation, with a decrease in the number and richness of mutualists (Francioli et al., 2022). The results presented here confirm these reports. An increase in the relative abundance of saprotrophic fungi from the genera *Trichoderma*, *Thalaromyces*, and *Schizothecium*, among others, was recorded. Among the saprophytes, an interesting observation is the appearance only in flooded F2 and F3 of the fungus from genus *Preussia* (0.3 and 0.6%, respectively). This is a fungus known mainly from animal faeces and leaf litter, but some representatives are also counted as endophytes (Massimo et al., 2015), and the sequence obtained in the present study is 98% similar to root endophytes in the non-mycorrhizal plant genus *Microthlaspi* (Glynou et al., 2016). At the same time, there was a decrease in the relative abundance of endophytic fungi such as *Darksidea* spp., and *Colletotrichum* spp.

Flooding is also associated with the presence of fungi in the soil that are potentially pathogenic to both plants and humans. In the present study, it was observed that the occurrence of plant pathogens is also related to soil type. The presence of fungi of the genus *Colletotrichum* (0.9, 0.1, 0.1%, in F1, F2 and F3, respectively) was recorded in all the soils, which disappeared as a result of flooding in F1 and F2, but in F3 its relative abundance increased to 0.4%. A similar observation applies to fungi of the genus *Fusarium*: in F1 they were not recorded after flooding, in F2 their relative abundance decreased from 0.8 to 0.7%, but in F3 it increased from 0 to 0.9%. A still different trend was noted for fungi of the genus *Alternaria*, all species of which are known as major plant pathogens (Pati et al., 2008). In F1, there was no change between present of this fungi in fresh and flooded soil. In F2 its relative abundance increased significantly from 0.06 to 0.51%. In contrast, in F3 the relative abundance of *Alternaria* decreased significantly from 1.17 to 0.08%. In F1, there was also a 10-fold (from 0.07 to 0.7%) increase in the relative abundance of *Parastagonospora* spp., whose representative, *P. nodorum,* is a major fungal pathogen of wheat (Richards et al., 2022). This indicates that the distribution of pathogens in soils as a result of flooding is also dependent on soil type and properties, and in the case of Fluvisols, very light type is more susceptible to an increase in the relative abundance of potentially pathogenic fungi.

Of all the identified fungi, representatives of 3 genera can be considered as indicators of excessive soil moisture: *Rhizoctonia*, *Entyloma*, and *Darksidea*. Representatives of these genera occurred only in fresh, natural Fluvisols, while they disappeared after flooding in all the investigated soils. This is interesting as *Rhizoctonia* (formerly *Thanatephorus*) representatives are known to be more active in high moisture conditions (Kumar et al., 2018). Their disappearance, on the other hand, is not negative, as most fungi of this genus and of the genus *Entyloma* are parasites and plant pathogens (Kruse et al., 2018; Pourmahdi, Taheri, 2015). In contrast, the disappearance of *Darksidea* as a result of flooding is a very undesirable effect, as fungi of this genus are among the most common members of the endophytic root fungal community in grassland and cereal ecosystems and have a positive effect on plant development (Knapp et al., 2015). At the same time, these are fungi associated with arid and semi-arid areas, so excess moisture can be detrimental to them (Khidir et al., 2010). In contrast, more than 20 genera, including *Acremonium*, *Mucor*, *Trichoderma*, *Inocybe*, *Entoloma*, *Clavaria*, *Cortinarius* and others, could be mentioned as specific core mycobiomes of Fluvisols from the Vistula River basin, which were present in all soils in both variants.

CONCLUSIONS

The impact of excessive moisture on the soil mycobiome and microbiome is incompletely understood. The present study confirms the few reports indicating that inundation causes significant restructuring of the soil mycobiome.

1. The excessive soil moisture caused by the simulated flood affects the structure of the soil mycobiome. The conditions of the simulated flood caused a decrease in diversity at the genus level in the mycobiome, which may affect the functioning of the environment.
2. Structure of the soil mycobiome is influenced by soil type and its physico-chemical properties.
3. Excessive moisture can contribute to the presence of pathogenic fungi in the soil, *e.g. Alternaria*, *Fusarium*.
4. We suggest that representatives of 3 genera fungi: *Rhizoctonia*, *Entyloma* and *Darksidea* might be indicators of excessive soil moisture.

However, the subject still needs to be researched and analysed, especially in natural conditions. Knowledge of the response of the mycobiomes in floodplains is essential to protect the functionality of these environments.

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