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REGULAR PAPER

Lignicolous fungal assemblages and relationships with environment in broadleaved and mixed forests from the North-East Region of Romania

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Background and aims – Lignicolous fungal assemblages perform numerous functions in forest ecosystems, one of the most important being their capacity to decay wood. As a consequence of their belonging to different ecological niches, the forest ecosystem influences the fungal assemblages in terms of species richness and composition.
Methods – In this study we analyzed the main lignicolous macrofungal assemblages in some deciduous and mixed deciduous-coniferous forests in the North-East Region of Romania. We searched to find fungal indicator species for a certain forest type and which are the main drivers and their effects on the composition of the lignicolous macrofungal assemblages. Fungal assemblages were identified using a hierarchical agglomerative clustering procedure, while diagnostic species for each cluster were identified based on the indicator value index. Relationships between fungal composition of plots and environmental variables were performed using detrended and canonical correspondence analyses.
Key results – A total of 377 fungal taxa in approximately 4600 records (in 59 plots) were identified. Six distinct clusters of lignicolous fungal assemblages were defined and separated three groups: 1) species-rich lignicolous fungal assemblages in beech forests (1 cluster), 2) well defined fungal assemblages in the mixed broadleaved-coniferous forests (2 clusters), and 3) fungal assemblages typical to oak forests (3 clusters). Ordination methods highlighted the forest type as the most important factor influencing the fungal composition of plots. Forestry Aridity Index, tree diversity and large trees basal area were also important factors for fungal assemblages but with a lower contribution.
Conclusion – In the studied region, fungal assemblages changed from oak to beech and to mixed, broadleaved-coniferous forests mainly as a consequence of different tree composition. Climate also shaped fungal composition but to a lesser extent.

Keywords – Forest type; wood inhabiting fungi; fungal composition; abiotic and biotic drivers.

INTRODUCTION

As components of all terrestrial ecosystems, fungal assemblages determine many important functions including nutrient cycling, carbon storage and productivity (Koide et al. 2011). Being probably the second-largest group of organisms on earth (Raja et al. 2017), fungi have multiple adaptations and response patterns to different ecosystem characteristics. They are the most important organisms which decay wood (Heilmann-Clausen & Christensen 2003), as they are able to degrade wood constituents, like lignin, cellulose and hemicellulose (Petre et al. 2014), thus being involved in the carbon cycle on the long term (Županić et al. 2009). In the context of climate change, the capacity of lignicolous fungi

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to decay wood assigned them even a higher ecological role (Diyarova 2016). Also, fungi present important functions in forest health (Heilmann-Clausen & Christensen 2003). As a consequence of their belonging to many ecological networks, the forest ecosystem's abiotic and biotic components are influencing, more or less, on long or shorter time, the fungal assemblages in terms of species richness and composition.

Fungal community ecology involves the study of species co-occurring in time and space (Koide et al. 2011). Since fungi cannot build self-sustaining communities (except for lichenized fungi), the fungal communities are linked to other organisms. Distinct assemblages of different species of fungi occupying similar habitats and shaped by distinct abiotic and biotic factors were emphasized. Identification of ecological factors with significant influence on the structure and composition of fungal communities is essential for habitat conservation or restoration and prediction of species responses to climate change (Koide et al. 2011). Depending on the functional group, some of the potentially important environmental factors for diversity and composition of assemblages of macrofungi were represented by moisture, temperature, pH and nitrogen concentration in the soil as well as tree size for the ectomycorrhizal fungi (Cavender-Bares et al. 2009; Koide et al. 2011; Kutszegi et al. 2015), while for the terricolous saprotrophic community, a litter pH gradient and tree species effects were detected (Kutszegi et al. 2015). Microclimatic conditions (Pouska et al. 2016) or species composition of living trees (Kutszegi et al. 2015) were highlighted as important factors for wood-inhabiting fungi. Also, the strong dependence of the diversity of lignicolous macrofungi on the presence, quantity and quality of dead wood was emphasized in numerous studies (Heilmann-Clausen 2001; Heilmann-Clausen & Christensen 2003; Küffer et al. 2008; Abrego & Salcedo 2011; Rudolf et al. 2012; Heilmann-Clausen et al. 2014; Kutszegi et al. 2015). Dead wood was emphasized as the most important microhabitat in forests, because the survival and development of numerous organisms depend on it (Heilmann-Clausen 2001; Abrego & Salcedo 2011; Goia & Gafta 2018).

These issues were investigated in a comprehensive study (Landi et al. 2015) showing that the vascular flora has a great potential to determine the diversity of other groups of organisms, such as fungi (heterotrophic organisms mainly dependent on vascular plants / plant materials), and that a relationship exists between the composition of communities of plants and fungi. Consistent correlations have been found between macrofungi and vascular plants, as those between the co-occurrence of *Fraxinus oxycarpa* and *Quercus petraea*, with distinct assemblages of ectomycorrhizal and saprotrophic fungi. As a consequence of fungal host preferences and habitat characteristics, specific assemblages of fungi were found in association with different tree and shrub species combinations. These results supported the hypothesis that the woody plant communities can be a useful indicator of the ectomycorrhizal (but not only) fungal communities; as a consequence, the strategies for conservation of fungi should aim at retaining diverse assemblages of host species and different structures across forests (Landi et al. 2015).

Dead wood characteristics are no doubt the most important driver for the composition of lignicolous macrofungal communities, e.g. diameter, decay stage, maximum decay stage, bark cover, log age, log complexity, substrate type (Heilmann-Clausen 2001; Heilmann-Clausen et al. 2005; Abrego & Salcedo 2011). Other factors were highlighted too, such as macro- and microclimate (Heilmann-Clausen 2001; Heilmann-Clausen & Christensen 2003; Heilmann-Clausen et al. 2005, 2014), soil humidity (Heilmann-Clausen 2001; Heilmann-Clausen & Christensen 2003; Heilmann-Clausen et al. 2005), relations with other organisms (moss cover, plant diversity: Heilmann-Clausen 2001; Heilmann-Clausen & Christensen 2003; Heilmann-Clausen et al. 2005), forest type (Heilmann-Clausen 2001; Heilmann-Clausen & Christensen 2003; Nordén et al. 2004; Heilmann-Clausen et al. 2005, 2014), topography (Heilmann-Clausen et al. 2014), etc.

In Europe dead-wood fungal communities have been extensively studied (Heilmann-Clausen 2001; Abrego & Salcedo 2011; Heilmann-Clausen et al. 2014; Kutszegi et al. 2015). But in Romania this group of organisms was neglected in most of the biodiversity studies and conservation projects, despite the ecological importance of macrofungi in forest ecosystems. Although some studies tried to document their diversity at the species level, there are very rare cases when plot-based sampling in combination with multivariate analyses were used in order to distinguish some macrofungal communities (Bîrsan et al. 2014), and there is practically no approach made in order to reveal the level of congruence between macrofungal communities and vascular plant communities and their relationships to environmental factors.

In this study it was expected to identify differences in the composition of lignicolous macrofungal communities depending on forest type and to characterize the relationship between biotic and abiotic site factors and community composition. For a number of macrofungal species, possible host preference (specific forest type) (via indicator species analysis) was also expected to be identified. Although fungi are integral components of natural communities, they are rarely used to characterize the latter, even though some fungal taxa could be better indicator species than plants because of their specificity to particular microhabitats and edaphic conditions. Their diagnostic usefulness as species indicators for certain forest communities was highlighted in North-American forests (Crabtree et al. 2010). Relationships between the diversity of plant and fungal communities were also highlighted, for example in the forests of Australia (Packham et al. 2002) where the macrofungal communities were much more species-rich than plant communities, in a 4:1 ratio. The presence of distinct communities of vascular plants and macrofungi with a high level of congruence was highlighted, but the variation in species composition was driven by different environmental variables compared to vascular plant communities.

This study tried to elucidate the following issues: (i) which are the main lignicolous macrofungal assemblages specific to some deciduous and mixed deciduous-coniferous forests in the North-East Region of Romania? (ii) are there fungal indicator species for a certain fungal assemblage? and, (iii) which are the main drivers and their effects on the composition of the lignicolous macrofungal assemblages in this region?

MATERIAL AND METHODS

Study area

Located in the North-East Region of Romania (from 46°6′10.58″N to 47°49′26.81″N and from 25°55′46.53″E to 27°41′6.6″E), the study area (fig. 1) covers approximately 36 488 km^2 (http://ec.europa.eu/eurostat/web/regions/data/database). The main geomorphological units are the Carpathians Mountains and the Moldavian Plateau with the Sub-Carpathians Hills in between (fig. 1), in an altitudinal range of 81–706 m a.s.l. In this area, the mean annual temperature ranges from 4°C to 11°C, while the mean annual precipitations decrease from 1000 to 600 mm as elevation is lower (ANM 2008). Main soil types are cambisols and luvisols. Vegetation is represented by various secondary grasslands and forests typical to the boreo-nemoral belt and to forest-steppe. The study area presents one of the highest forest cover (ca. 12 122 km^2) among all development regions of Romania, (Andronache et al. 2017). In forest-steppe and sub-mountainous areas the main forest types are dominated by the broadleaved species of *Quercus* and *Fagus*, while in the mountainous regions *Picea abies* edifies pure and mixed broadleaved-coniferous forests mainly with *Fagus sylvatica* and *Abies alba* (Chifu et al. 2006). Deforestation and illegal logging (Bouriaud 2005; Andronache et al. 2017) expose these forest habitats to high anthropic pressure. This type of management and wood extraction have often been seen as a decreasing factor for lignicolous fungi diversity. Also, the reduction of wood quantity influences fungal assemblages by decreasing dissimilarities among communities and by simplifying their structure (Heilmann-Clausen & Christensen 2003).

In order to find the drivers shaping the composition of lignicolous fungal assemblages across forests in the North-East Region of Romania, various biotic, climatic and topographic variables were analysed (table 1).

Biotic variables

Forest structural indicators were assessed in 59 randomly chosen circular plots of 1000 m^2 in oak, beech and mixed beech-spruce forests across study area. Within plots, each tree larger than 10 cm diameter at breast height (DBH) was identified and DBH was registered. For each plot the Shannon diversity of trees as well as the basal area of mature trees (DBH > 40 cm) were calculated. Coarse woody debris (CWD – woody debris with diameter over 10 cm) represented by stumps, snags, logs and large branches were investigated for diameter (both ends diameter for logs and large branches; upper diameter for stumps; DBH for snags), tree species and decay stage. Decay stage (supplementary file 1) was assessed following a modified classification of Heilmann-Clausen & Christensen (2003) for lying woody debris, Tavankar et al. (2014) for snags, and Lombardi et al. (2013) for stumps. Downed coarse woody debris (DCWD) genera and decay stages richness were calculated using volumes for logs and large branches (Runnel & Lõhmus 2017). Number of fine woody debris (FWD – woody debris with diameter under 10 cm), number of stumps, and DCWD volume were also calculated to represent the dead wood pool availability.

For each investigated forest stand the following specific variables were calculated: tree total basal area, tree density, tree mean basal area, tree DBH coefficient of variation, and basal area of large living trees. Large snags total basal area and snags density were also calculated, because snags have been shown to be of great importance for fungi (Çolak et al. 2010). Forest type was the only qualitative variable, all the plots being assigned to the three studied major forest habitats: oak, beech, and beech-coniferous forests.

Abiotic variables

Climatic factors were represented by temperature seasonality, temperature annual range and precipitation seasonality downloaded from WorldClim 2.0 database at 30 arcsec (ca. 1 km) resolution (Fick & Hijmans 2017) and by snow cover length downloaded from Lifewatch-WB ecotope database (Lifewatch 2019) at 500 m resolution. Forestry Aridity Index (FAI) was calculated in order to highlight the relation between aridity and dominant trees in forests (Führer et al. 2011). Topographic variables were represented by slope, aspect index (ASPI) after Wang et al. (2015), and Positive Openness (PO). Raster-derived variables were processed using SAGA GIS software (Conrad et al. 2015).

Fungal data collection

Lignicolous fungi were assessed in 59 circular plots of 2000 m^2, superimposed on plots made in order to characterize the forest structure. Most of fungal species were identified directly in site. For problematic species, the sporomes were collected and identified in laboratory using literature (Ellis & Everhart 1966; Ryvarden 1976; Breitenbach & Kränzlin 1986; Gilbertson & Ryvarden 1986, 1987; Jülich 1989; Ryvarden 1991; Ryvarden & Gilbertson 1994; Senn-Irlet 1995; Gerhardt 1999; Vasilyeva et al. 2007; Tănase et al.

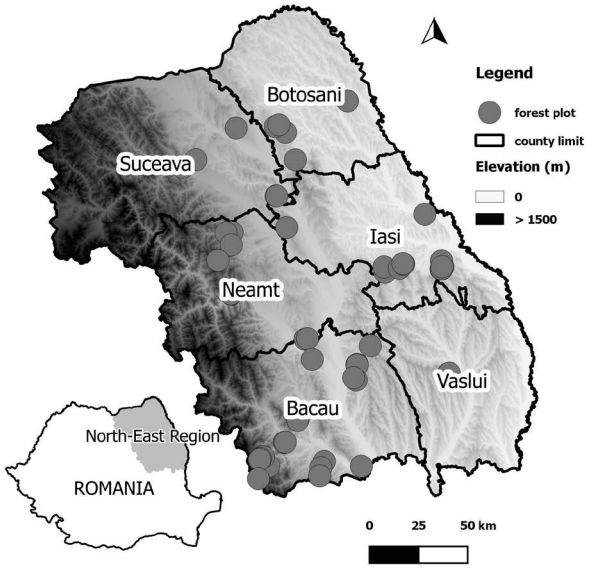

Figure 1 – Map presenting the distribution of plots in the forests from the North-East Region of Romania.

Table 1 – Descriptive statistics of environmental and forest stand variables used in the analysis of lignicolous fungal assemblages in the North-East Region of Romania.
Beech forests – 23 plots; Mixed forests – 10 plots; Oak forests – 26 plots.

Variable	Abbreviation	Mean	Min	Max	SD
Aspect Index	ASPI	82.94	2.44	174.29	49.03
Decay diversity of DCWD	DCWD_DECAY	0.3	0	0.98	0.34
Taxonomic diversity of DCWD	DCWD_DIV	0.23	0	1.08	0.33
DCWD volume	DCWD_VOL	11.79	0	148.88	24.39
Forestry Aridity Index	FAI	4.98	3.9	6.1	0.59
FWD number of of pieces	FWD	30.17	14	63	10.76
Total basal area of large snags	LARGE_SNAG_BA	1.33	0	13.73	2.82
Total basal area of large trees	LARGE_TREE_BA	63.65	0	97.88	27
Positive Openness Index	PO	1.46	1.17	1.57	0.07
Snow Cover Length	SCL	10.25	3	18	3.93
Slope	SLOPE	10.21	0.7	30.4	7.27
Number of snags	SNAG_N	19.49	0	120	22.08
Number of stumps	STUMP_N	44.07	0	190	37.47
Total basal area of trees	TREE_BA	39.5	17.4	68.29	12.25
Tree DBH coefficient of variation	TREE_DBH_CV	0.92	0.34	1.92	0.36
Tree diversity (Shannon)	TREE_DIV	0.98	0	1.67	0.43
Tree density	TREE_N	345.08	120	810	140.79

2009; Courtecuisse & Duhem 2013). Species nomenclature follows Index Fungorum (http://www.indexfungorum.org/Names/Names.asp). Voucher specimens were deposited in the herbarium of Faculty of Biology, Alexandru Ioan Cuza University (Romania). Sporomes were sampled at least three times per each plot, from late spring (May) to mid-autumn (October).

Data analysis

Lignicolous fungal assemblages were identified using a hierarchical agglomerative clustering procedure, by applying the flexible ß clustering algorithm (ß = −0.25) and Bray-Curtis distance on presence-absence dataset. After cutting the output dendrogram into nine partitions (2–10 clusters), the optimum number of clusters was identified using the mean Silhouette index and the corrected Rand index (Rand 1971; Hubert & Arabie 1985). Diagnostic species for each cluster were identified based on the indicator value index (Dufrêne & Legendre 1997). Rare species occurring in 1–2 plots were removed. Clustering analysis was carried out using version 3.5.1 of the statistical programming environment R (R Core Team 2018) by applying packages base, cluster (Maechler et al. 2018), indicspecies (de Cáceres & Legendre 2009), vegan (Oksanen et al. 2018) and reshape2 (Wickham 2007). For graphical representation we used R packages ggplot2 (Wickham 2016) and RColorBrewer (Neuwirth 2014).

The relationships between fungal composition of plots and environmental variables were performed in CANOCO 5 software (ter Braak & Šmilauer 2002), using detrended correspondence analysis (DCA) on presence-absence data, detrending by segments and down-weighting rare species. The effect of each variable on the fungal composition was highlighted in a canonical correspondence analysis (CCA) with forward selection of variables and Monte Carlo test (9999 iterations). Numerical variables were checked for collinearity using Pearson correlation.

RESULTS

Species composition

In this study 374 taxa in ca. 4600 records (in 59 plots) were recorded. The species were classified in 197 genera, 82 families, 30 orders and 2 phyla. Most of them belonged to Basidiomycota phylum (83.9%), while the remaining to Ascomycota (16.1%). Among ascomycetes, the most frequent taxa were *Diatrype stigma*, *Jackrogersella cohaerens*, *Hypoxylon fragiforme*, *Nemania serpens*, *Xylaria polymorpha*, *Diatrypella* agg., *Hypoxylon rubiginosum*, *Biscogniauxia nummularia* and *Kretzschmaria deusta*. The most common basidiomycetes were *Stereum hirsutum*, *Exidia glandulosa*, *Schizophyllum commune*, *Marasmius rotula*, *Hymenopellis*

Table 2 – **Diagnostic species (significantly associated to the clusters resulting from hierarchical clustering, with indicator values and P-values < 0.05).**

Variable	Indicator value	P
Cluster 1		
Melogramma spiniferum (Wallr.) De Not.	0.646	0.002
Kretzschmaria deusta (Hoffm.) P.M.D.Martin	0.544	0.024
Diatrype disciformis (Hoffm.) Fr.	0.537	0.019
Bjerkandera adusta (Willd.) P.Karst.	0.525	0.002
Biscogniauxia nummularia (Bull.) Kuntze	0.503	0.046
Pluteus nanus (Pers.) P.Kumm.	0.466	0.05
Cluster 2		
Phellinus hartigii (Allesch. & Schnabl) Pat.	0.926	0.001
Heterobasidion annosum (Fr.) Bref.	0.816	0.001
Pseudohydnum gelatinosum (Scop.) P.Karst.	0.772	0.001
Trichaptum abietinum (Pers. ex J.F.Gmel.) Ryvarden	0.737	0.001
Peniophora piceae (Pers.) J.Erikss.	0.726	0.001
Ganoderma applanatum (Pers.) Pat.	0.719	0.001
Tricholomopsis rutilans (Schaeff.) Singer	0.665	0.004
Mycetinis alliaceus (Jacq.) Earle ex A.W.Wilson & Desjardin	0.643	0.005
Fomitopsis pinicola (Sw.) P.Karst.	0.630	0.002
Bertia moriformis (Tode) De Not.	0.600	0.007
Trichaptum biforme (Fr.) Ryvarden	0.591	0.004
Hypholoma capnoides (Fr.) P.Kumm.	0.587	0.006
Mucidula mucida (Schrad.) Pat.	0.573	0.011
Chlorociboria agg.	0.568	0.018
Pluteus phlebophorus (Ditmar) P.Kumm.	0.555	0.017
Eutypa spinosa (Pers.) Tul. & C.Tul.	0.552	0.031
Jackrogersella cohaerens (Pers.) L.Wendt, Kuhnert & M.Stadler	0.543	0.001
Hypoxylon rubiginosum (Pers.) Fr.	0.539	0.034
Cluster 3		
Stereum gausapatum (Fr.) Fr.	0.741	0.001
Mycena hiemalis (Osbeck) Quél.	0.722	0.002
Xylobolus frustulatus (Pers.) P.Karst.	0.722	0.003
Lycoperdon perlatum Pers.	0.613	0.005
Mycena tenerrima (Berk.) Quél.	0.596	0.013
Dialonectria episphaeria (Tode) Cooke	0.582	0.01
Panellus stipticus (Bull.) P.Karst.	0.565	0.021
Hymenochaete rubiginosa (Dicks.) Lév.	0.559	0.013
Mycena corticola (Pers.) Gray	0.526	0.029
Hypholoma fasciculare (Huds.) P.Kumm.	0.521	0.049
Calocera viscosa (Pers.) Fr.	0.519	0.038
Hypoxylon fragiforme (Pers.) J.Kickx f.	0.512	0.024

Table 2 (continued) – Diagnostic species (significantly associated to the clusters resulting from hierarchical clustering, with indicator values and P-values < 0.05).

Variable	Indicator value	P
Cluster 4		
Fuscoporia ferruginosa (Schrad.) Murrill	0.624	0.005
Phellinus pomaceus (Pers.) Maire	0.624	0.006
Phlebia radiata Fr.	0.602	0.009
Mycena niveipes (Murrill) Murrill	0.577	0.013
Dendrothele acerina (Pers.) P.A.Lemke	0.567	0.01
Fuscoporia contigua (Pers.) G.Cunn.	0.566	0.013
Irpex lacteus (Fr.) Fr.	0.552	0.017
Cyathus striatus (Huds.) Willd.	0.551	0.008
Peniophora quercina (Pers.) Cooke	0.530	0.04
Gymnopus fusipes (Bull.) Gray	0.510	0.041
Exidia glandulosa (Bull.) Fr.	0.503	0.049
Cluster 5		
Lentinus arcularius (Batsch) Zmitr.	0.716	0.001
Daedalea quercina (L.) Pers.	0.679	0.002
Cluster 6		
Laetiporus sulphureus (Bull.) Murrill	0.660	0.002
Hypoxylon fuscum (Pers.) Fr.	0.629	0.001
Peniophora limitata (Chaillet ex Fr.) Cooke	0.613	0.004
Megacollybia platyphylla (Pers.) Kotl. & Pouzar	0.577	0.01
Coprinellus domesticus (Bolton) Vilgalys, Hopple & Jacq.Johnson	0.576	0.011
Nectria cinnabarina (Tode) Fr.	0.564	0.017
Coprinellus disseminatus (Pers.) J.E.Lange	0.560	0.023
Vuilleminia comedens (Nees) Maire	0.553	0.01
Mycena rosea Gramberg	0.543	0.015
Hyphodontia quercina (Pers.) J.Erikss.	0.520	0.036

radicata, *Bjerkandera adusta*, *Trametes versicolor*, *Fomes fomentarius*, *Peniophora quercina*, *Pluteus cervinus* etc. Some species rich fungal families were highlighted, such as Polyporaceae (9.3% of total richness), Mycenaceae, Hymenochaetaceae, Pluteaceae and Meruliaceae. From the Red List of Romanian Macrofungi (Tănase & Pop 2005), 9 species have been found: *Coprinopsis alopecia*, *Grifola frondosa*, *Hymenochaete cruenta*, *Lycoperdon echinatum*, *Mutinus caninus*, *Mycena crocata*, *Pluteus petasatus*, *P. salicinus* and *Rickenella fibula*.

The species richness per plot ranged from 18 to 73 (with a mean of 46). 105 fungal species were recorded in only one plot, while 222 species were identified in more than two plots, and used for further analysis. In total, 59 species had a significant indicator value for a certain cluster, representing ca. 15.77% of total richness of plots (table 2). All lignicolous fungal assemblages in beech forests were defined by species with high indicator value (e.g. *Bjerkandera adusta*, *Diatrype disciformis*, *Jackrogersella cohaerens*, *Kretzschmaria deusta* and *Melogramma spiniferum*). Mixed coniferous forests were well characterized by *Xylobolus frustulatus*, *Phellinus hartigii*, *Heterobasidion annosum*, *Pseudohydnum gelatinosum* while the fungal assemblages in thermophilous oak forests were defined by the lowest number of indicator species (*Lentinus arcularius* and *Daedalea quercina*).

Lignicolous fungal assemblages and relationships with environment

Hierarchical clustering algorithm generated a dendrogram which was cut into 9 partitions with 2−10 clusters (fig. 2). Corrected Rand index had the highest values between partitions with 6 and 7 clusters. The Silhouette index showed a local maximum for the partition with 6 clusters, and consequently, the optimum number of clusters taken into consideration was 6 (fig. 2). In this way were separated species-rich

lignicolous fungi assemblages in beech forests (Cluster 1) from the Moldavian Plateau, well defined fungal assemblages in the mixed broadleaved-coniferous forests from the Carpathian Mountains (Clusters 2, 3) and fungal assemblages more typical to oak forests in lower areas and riparian forests (Clusters 4, 5, 6).

Within the DCA (fig. 3), the first two axes accounted for 41.4% of variation, axis one accounting for 26.5%, which is an indicator of high explanatory power compared with axes 2 and 3, with respectively 14.9% and 11.6%. DCA analysis highlighted the pronounced effect of the forest type, structure and vitality (by the dominant tree species, large trees basal area, large snags basal area, or dead wood characteristics) on fungal species composition in recorded plots and represented the main gradient along Axis 1. Also, Axis 1 was correlated with climatic-related factors as the positive openness or snow cover length and slope. Axis 2 was correlated with forest aridity, tree diversity and stump and trees densities. Thus, Axis 1 was more related to substrate properties and quality, the fungal composition changing from the oak forests to pure beech and to mixed beech-coniferous forests. Axis 2 was a gradient of forest aridity and structure, the fungal composition of plots changing from mixed forest (with low values of aridity index) to broadleaved forests (with increased values of the same index).

The CCA analysis highlighted the forest type as the most important factor influencing the fungal composition of plots in the studied region. Forestry Aridity Index, tree diversity and large trees basal area were also important factors for fungal assemblages but with a lower contribution (table 3).

DISCUSSION

Lignicolous fungal communities

Beech forests – Cluster 1 – In the beech forests of the Moldavian Plateau, the Moldavian Sub-Carpathians and the southeastern region of Romanian Eastern Carpathians species-rich lignicolous fungal assemblages were identified. These forest stands were distributed on nutrient rich, neutral soils and are mainly classified into *Lathyro hallersteinii-Carpinion* Boșcaiu et al. 1982 phytosociological alliance. They are characterized by high climatic and topographic variability, and also by the significant differences in wood quality and quantity. Still, beech (*Fagus sylvatica*) was the dominant element in terms of stand structure and composition as well as woody debris. Species richness of lignicolous fungi was higher compared to all other assemblages but this might be related with the fact that it groups the largest number of plots. These fungal assemblages were well defined by diagnostic species frequently found on beech wood such as *Diatrype disciformis*, *Biscogniauxia nummularia*, *Bjerkandera adusta*, *Kretzschmaria deusta* etc. Some of these species, particularly in Aphyllophorales and Pyrenomycetes have long-lasting fruit bodies (Abrego et al. 2016; Purhonen et al. 2017) or have extended fruiting periods (Frankland et al. 1982) and can be used as beech forests indicators (as in this case) and as surrogate candidates for conservation management (Halme et al. 2016).

Mixed (broadleaved-coniferous) forests – Clusters 2, 3 – Well defined fungal assemblages were identified in the mixed broadleaved-coniferous forests from the Carpathian Mountains which syntaxonomically correspond to the *Symphyto cordati-Fagion sylvaticae* Vida 1963 alliance. Their stands were characterized by ideal conditions for existence of high fungal diversity, because higher precipitations and lower temperatures maintain high substrate humidity. Coniferous tree species, as the fir (*Abies alba*) or spruce (*Picea abies*) represented the source of a great amount of high quality coarse woody debris. Among the broadleaved tree species, the beech (*Fagus sylvatica)* was co-dominant. Locally, where the sessile oak (*Quercus petraea*) dominated the cover (up to 40%), it was accompanied by a significant number of fungi species preferring the oak wood. This was the main reason of separating two groups of lignicolus fungi: one preferring mainly beech wood and the second preferring mainly oak wood, but both in the general background of coniferous forests. Their high species richness was facilitated by favour-

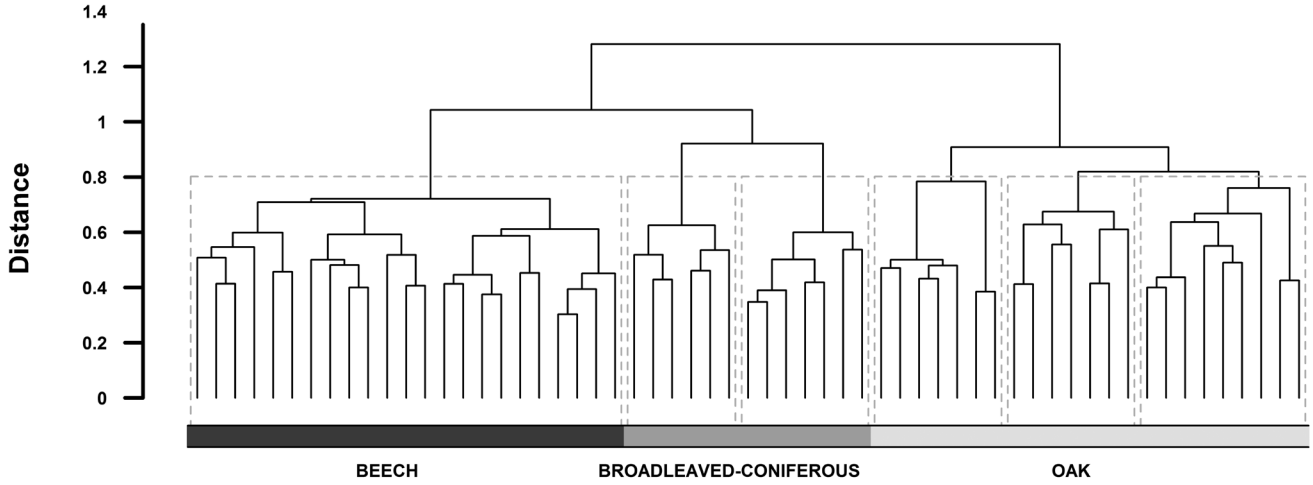

Figure 2 – Dendrogram of numerical classification of fungal assemblages (generated via hierarchical clustering of 59 plots in different forest ecosystems). The main forest types (beech, oak and broadleaved-coniferous) are highlighted.

Table 3 – **Results of the forward selection in CCA ordination and effects of biotic and abiotic variables on the composition of fungal assemblages.**
Full names of variables ar available in table 1.

Variable	Explains %	Contribution %	Pseudo-F	P-value	P-value (adj.)
FOREST = mixed	5	12.7	3	0.0001	< 0.005
FOREST = beech	3.4	8.7	2.1	0.0001	< 0.005
FOREST = oak	3.4	8.7	2.1	0.0001	< 0.005
LARGE_TREE_BA	2.4	6	1.5	0.0007	< 0.05
SNAG_N	2.3	5.8	1.4	0.0039	ns
TREE_DIV	2.3	5.7	1.4	0.001	< 0.05
FAI	2.3	5.7	1.4	0.001	< 0.05
FWD	1.8	4.5	1.1	0.1485	ns
ASPI	1.8	4.5	1.1	0.1384	ns
DCWD_DECAY	1.7	4.4	1.1	0.2133	ns
SCL	1.8	4.4	1.1	0.1864	ns
POI	1.7	4.4	1.1	0.2256	ns
DWCD_DIV	1.7	4.4	1.1	0.2338	ns
TREE_BA	1.8	4.5	1.1	0.1562	ns
SLOPE	1.8	4.5	1.1	0.1945	ns
STUMP_N	1.6	4.2	1.1	0.3414	ns
LSNAG_BA	1.7	4.2	1.1	0.3234	ns
TREE_N	1.6	4.1	1	0.3892	ns
TREE_DBH_CV	1.5	3.8	1	0.5788	ns
DCWD_VOL	1.4	3.6	0.9	0.6441	ns

able climatic conditions and higher tree diversity. Also, high inclination values typical to mountain landscape might have favoured CWD accumulation at slope base, increasing lignicolous fungal diversity (Sefidi et al. 2016).

The ecological profile of component species indicates the high variety of ecological niches found in these forests. Some diagnostic species for fungal assemblages (Cluster 2) in the studied beech-spruce forests (e.g. *Phellinus hartigii* or *Heterobasidion annosum*) were known sapro-parasites of *Abies* and *Picea* trees (Hennon & Mulvey 2014) while others were well known coniferous-associated saprotrophs (e.g. *Peniophora piceae*, *Pseudohydnum gelatinosum*, *Trichaptum abietinum*, *Tricholomopsis rutilans*, *Hypholoma capnoides* (Breitenbach & Kränzlin 1986; Tănase et al. 2009; Bernicchia & Gorjón 2010; Luchi et al. 2015). Some lignicolous macromycetes colonized freshly dead wood, such as *Trichaptum abietinum* (Breitenbach & Kränzlin 1986), or wood in various decay stages (*Pseudohydnum gelatinosum;* Zabel & Morrell 1992). Some species were found especially on logs – *Phellinus hartigii*, *Pseudohydnum gelatinosum* (Breitenbach & Kränzlin 1986) – while others on stumps, such as *Hypholoma capnoides*, *Tricholomopsis rutilans* (Eyssartier & Roux 2013). Numerous diagnostic species preferred beech wood: *Mycetinis alliaceus*, *Mucidula mucida*, *Eutypa spinosa* and *Jackrogersella cohaerens* (Eyssartier & Roux 2013; Kutszegi et al. 2015; Müller et al. 2007; Vasilyeva et al. 2007). The diagnostic species for Cluster 3 (assemblages in sessile oak-coniferous forests) belonged to ephemeral genera like *Mycena* sp. and *Calocera* sp. Another diagnostic species for this cluster, *Xylobolus frustulatus*, usually occurs in oak old-growth forests of Europe, especially on big logs or stumps (Stasińska 2008). Also, *Hymenochaete rubiginosa* and *Stereum gausapatum* identified on the oak dead wood, were emphasized as preferring this substrate type (Breitenbach & Kränzlin 1986; Kutszegi et al. 2015).

Oak forests – Clusters 4, 5, 6 – Oak-dominated forests are harbouring three distinct fungal assemblages: assemblages in general oak forests in nemoral belt, assemblages in thermophilic oak forests, and assemblages in mesophilic riparian oak forests.

Cluster 4 comprised plots of high species richness distributed in mixed oak-hornbeam-beech forests from the Moldavian Plateau and the Sub-Carpathians, included in *Lathyro hallersteinii-Carpinion* Boșcaiu et al. 1982 phytosociological alliance. These assemblages hosted the second lignicolous fungal richness among communities, probably due to

the largest altitudinal, thermic and CWD volume amplitude. It had the largest oak CWD volume, the largest hornbeam tree proportion but the lowest beech one, thus the dead wood profile was dominated by oak and hornbeam. Some of the diagnostic species were consequently associated with oak – *Peniophora quercina*, *Gymnopus fusipes*, *Exidia glandulosa* f. *truncata* (Breitenbach & Kränzlin 1986; Eyssartier & Roux 2013). Most of the diagnostic (indicator) species were found on FWD, indicating that in case of ecological niche variation, diagnostic species will be delineated by the most common type of woody debris, which in this case was oak FWD. Because the FWD is directly related to tree species composition, even in different macroclimatic conditions (which are known to influence FWD decay, and subsequently, fungal communities) the presence of diagnostic species can be linked to forest composition.

Cluster 5 contained species-poor fungal assemblages (the lowest richness of all plots) identified in thermophilic and relatively young oak forests (*Quercion petraeae* Zólyomi & Jakucs 1957) from Dealul Mare-Hârlău area and the Bârlad Plateau. It was the poorest habitat in terms of total DCWD volume, tree diversity and decay stages diversity. Therefore, the lignicolous fungi tended to develop especially on FWD, often under strong xeric conditions. The number of diagnostic species was low, only two species having strong preference for this forest type: *Lentinus arcularius* and *Daedalea quercina*, both oak-associated (Breitenbach & Kränzlin 1986; Tănase et al. 2009). The second species highlighted also the anthropogenic influence through CWD collecting, because, in this study, it was found exclusively on cut stumps.

Cluster 6 included fungal assemblages from riparian forests of *Quercus robur* with *Ulmus* sp. and *Fraxinus* sp. on the Bârlad Plateau, on recent alluvial deposits, usually classified in the *Ulmenion* Oberd. 1953 alliance. These were old-growth oak forests with the highest tree diversity, located at low elevation. The macroclimate was characterized by highest mean annual temperatures and lowest mean precipitations, while De Martonne Aridity Index suggested pronounced xeric conditions. However, the investigated forests were located in the major riverbed of some rivers and were exposed to flooding during the period of rising water level. Thus, local topographic features indicated long periods of water level close to surface. Many lignicolous fungi species were identified on FWD and logs which were often in close contact with very wet soils. Although the diagnostic species occupied various ecological niches, both in terms of tree preferences and dead wood quality, still they were related to forest humidity. *Crepidotus mollis* was often reported from alluvial forests in Central and Western Europe (Senn-Irlet 1995), while *Peniophora limitata* was frequently associated with water-loving trees like ash (*Fraxinus* sp.) (Breitenbach & Kränzlin 1986). *Hypoxylon fuscum* was also found in other hardwood floodplain forests (Jančovičová & Glejdura 1999) and *Laetiporus sulphureus* in alluvial oak forests (Bîrsan et al. 2014) or alluvial alder forests (Mihál & Blanár 2014).

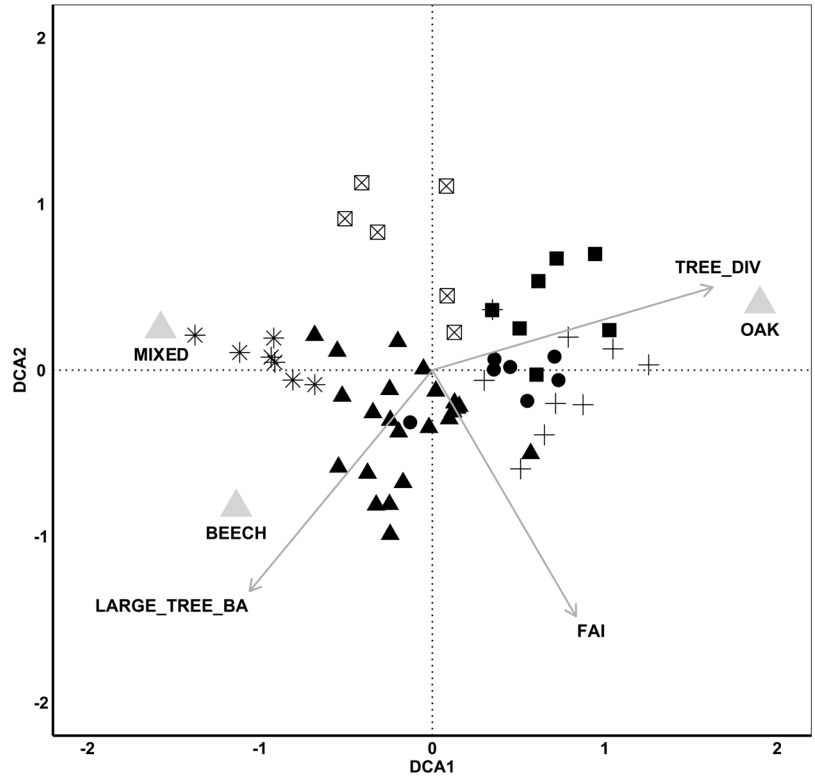

Figure 3 – DCA of the 59 plots. Only first 2 axes are presented and only significant environmental factors according to CCA are passive projected onto DCA ordinogram. Fungal assemblages are symbolized according to their classification in hierarchical clustering: black triangle = Cluster 1; star = Cluster 2; crossed-square = Cluster 3; black square = Cluster 4; black circle = Cluster 5; cross = Cluster 6. Eigenvalues: Axis 1 – 0.2617, Axis 2 – 0.1629. Length of gradient along Axis 1 – 2.63.

Relationships between fungal assemblages and environmental factors

Forest type – In this study, forest type was highlighted as the most important factor that explains the variation of lignicolous fungal composition in sampled forests (table 3). Thus, fungal composition changed from oak-dominated to beech-dominated and to mixed broadleaved-coniferous forests, as a consequence of different forest tree composition. Dominant tree species were emphasized as the main drivers of lignicolous fungal composition in beech and oak-dominated forests from Western Hungary (Kutzegi et al. 2015). Dominant or co-dominant tree species had a particular importance because it was the most significant supplier of dead wood in a certain forest type. Depending on tree species, dead wood had different physical and chemical properties and was colonized by different fungal species. Based on their affinity (habitat preference) for a certain forest type, they were considered as indicator species. A part of these species (e.g. *Daedalea quercina*, *Peniophora quercina*, *Laetiporus sulphureus*, *Hymenochaete rubiginosa*) were confirmed as indicator for fungal assemblages in other studies carried out in oak forests from Central and Eastern Europe – Hungary (Kutszegi et al. 2015) or Romania (Bîrsan et al. 2014). In addition, *Kretzschmaria deusta*, *Diatrype disciformis* and *Biscogniauxia nummularia* were highlighted as indicator for fungal assemblages in beech forests from Romania (Bîrsan et al. 2014), Spain (Abrego & Salcedo 2011) or Hungary (Kutszegi et al. 2015).

Some of the indicator species for mixed broadleaved-coniferous forests in our study, as *Mycetinis alliaceus*, *Mucidula mucida*, *Trichaptum biforme*, were also found indicators for beech forests in Hungary (Kutszegi et al. 2015) or Spain (Abrego & Salcedo 2011). The fact that a particular species had a slightly different preference for forest habitat might be a consequence of regional climatic differences. In Hungary, for example, the beech-dominated forests were distributed in areas with high precipitations and lower mean temperatures (Kutszegi et al. 2015), similar to climatic particularities of beech-coniferous forests in low mountains of the North-East Region of Romania. This demonstrates that lignicolous macromycetes tend to associate with a specific forest type, under similar climatic conditions.

Forestry Aridity Index – Another significant factor, Forestry Aridity Index (FAI), showed that fungal composition changes from mountain areas to hilly and plain areas. Low values of FAI are typical for mountain areas and are associated with broadleaved-coniferous forests (Führer et al. 2011). The importance of FAI for fungal assemblages consists in its relationship with the total mass of organic matter, which is higher in stands from cooler and wetter climate (Führer et al. 2011). In this study, low FAI values were associated to fungal communities located in mountain forests characterized by high niche variation, increased resource and substrate specificity variation. The species-rich assemblages in these forests were associated to higher substrate volume. Mountain forest stands benefited from more humidity, which induced higher substrate humidity and corroborated with lower temperatures, increased macrofungal richness and determined composition variability. Colder climate is known to decrease decomposition speed (Lombardi et al. 2013). Consequently, the volume of dead wood in mountainous forest stands is increasing and also the decay stages, highly influencing turnover of fungal communities (Heilmann-Clausen et al. 2005).

Another aspect refers to the microclimatic conditions specific to vegetation growth period. During this period, the forest canopy was well developed and little solar radiation reached the soil, increasing substrate humidity. In fact, in beech-coniferous and spruce forests from Germany, Bässler et al. (2010) found that sun exposure, soil humidity and sapling cover acted as a microclimatic factor group, influencing fungal composition, especially on FWD. Sensitivity to microclimatic variations of fungal species on very fine woody debris (dead wood with diameter under 5 cm) was also highlighted for beech twigs from the North-East Region of Romania (Copoț et al. 2018).

Tree diversity (Shannon) – Living trees diversity was also a significant factor shaping the fungal composition in the studied forest types, determining a shift from the almost pure beech forests (with low tree diversity) to oak-dominated forests (with 5–6 species in tree layer). The change in composition of lignicolous fungi was directly linked to FWD taxonomic diversity and consequently to more available ecological niches. This allowed different macrofungi species to develop separately on different taxonomic substrates, avoiding interspecific competition, and grouping in different fungal assemblages. In this respect, tree diversity acted more like a nutrient type gradient. More FWD diversity (~tree diversity) might sustain diverse fungal composition, as Kubartová et al. (2009) found. Various combinations of highly diverse plant debris indicated a higher litter fungal composition in oak-dominated forests in France (Kubartová et al. 2009). Many saprotrophic macromycetes are migrating through litter in search of new microhabitat (Boddy 1993), explaining the high percentage of soil fungal communities found also on wood in boreal forests (Mäkipää et al. 2017). Intimate contact of dead wood with litter was assumed to increase substrate humidity (Heilmann-Clausen & Christensen 2003), with positive effects on diversity of lignicolous fungal. Also, the long-lasting humidity in the substrate, created better opportunities for more fungi to develop on all types of downed wood, increasing fungal alpha and beta diversities not only on CWD but also on FWD, contrary to the general opinion of CWD-leading role (Heilmann-Clausen et al. 2005).

Because wood extraction decreases dead wood availability in forests, the fungi preferring DCWD are more vulnerable compared to those on FWD. This explained the existence of forests with very low DCWD taxonomic diversity and high tree diversity in the investigated area and also with increased FWD. This means that the DCWD diversity was not a reflection of tree diversity in oak-dominated habitats from non-mountainous regions. Less DCWD diversity might favour particular fungal species, known to grow on FWD, like *Fuscoporia contigua*, *Vuilleminia comedens*, *Peniophora quercina*, *Lentinus arcularius* (Bernicchia & Gorjón 2010) or on stumps, like *Panellus stipticus*, *Daedalea quercina*, *Mycena inclinata* coming from oak trees (Bîrsan et al. 2014). In beech-dominated forests, the community was strictly related to beech wood, as most of diagnostic species found there were known to frequently colonize beech substrates.

Similarities and differentiations between fungal communities could be also observed depending on substrate type. Thus, *Peniophora limitata* and *P. quercina* were identified on branches, often attached to tree (Boddy et al. 1987), occupying the same niche in slightly different oak-habitats. Also, a specific sapro-parasitic macrofungal species was identified in all oak-dominated forests: *Cerioporus squamosus* in oak forest from nemoral region, *Phellinus igniarius* in riparian oak forests, and *Daedalea quercina* in thermophilic ones. All these species have the enzymatic equipment to colonize multiple hosts but developed preferences for a particular tree genus. These species, adapted to different substrate types, avoided interspecific competition and established themselves as main wood-decay and aggressive parasites in the studied oak forests. Their combative dominance as wood pathogens was favoured by their presence on living trees before tree falling/disintegration (Holec et al. 2019).

Mature trees total basal area – Fungal composition of plots changed along a gradient of forest age structure from young oak-dominated forests, to mature beech forests, and to old-growth beech-fir forests. The importance of big mature trees was often highlighted in studies on old-growth forests, described as habitats with great fungal diversity (Dvořák et al. 2017; Runnel & Löhmus 2017), largely because of the high availability of coarse wood debris (Brunet et al. 2010). Thus, lignicolous fungi aggregate in communities, at different scales, due to niche variation, from each woody debris piece to stand level. This situation was also observed in the current study, the beech-spruce-fir associated fungal community (Cluster 5) was characterized by highest DCWD quality (taxonomic and decay stages) and quantity (DCWD volume) and fungal diversity. In the composition of the fungal assemblages from old broadleaved-coniferous forests from the Carpathians, some indicator species were confirmed for other European old-growth forests: *Mycena hiemalis*, *Pluteus phlebophorus* etc. Other indicator species for old-growth forests were also found in this study, either in beech forests, as *Phleogena faginea*, *Pluteus nanus*, *P. umbrosus*, *Hypocrea gelatinosa*, *Flammulaster muricatus* (Dvořák et al. 2017) or oak forests, as *Oxyporus corticola* (Runnel & Löhmus 2017).

Conclusion

This study adds new insights to assemblages of lignicolous fungi in a less-studied part of Europe. It is the first study at regional scale in Romania, dealing with the relationships between forest environment and fungal species at community level. This investigation highlighted the tree species composition, substrate characteristics and climate as the factors driving assemblages of lignicolous fungi in the study area. The composition of these assemblages showed a significant change from oak to beech, and to deciduous-coniferous forests mainly due to dominant tree species. Also, tree diversity, stand age and climate explained changes in fungal species composition but with minor contribution. Generally, the assemblages were composed by fungi that are known to develop strong associations with a dominant tree, particularly because of their enzymatic adaptations to different chemical and physical properties of wood. Overall, the composition of lignicolous fungal changed at regional scale, based on gradients of forest composition and structure. For conservation purposes, it is important to maintain natural old forests, with important amounts of dead wood, in order to enhance the chances for fungal communities to survive and perform their ecological role in the forest environment.

SUPPLEMENTARY FILE

One supplementary file is associated to this paper:

Classification of decay stages for logs and large branches (DCWD), stumps and snags (pdf):
https://doi.org/10.5091/plecevo.2020.1688.2031

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