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...
Dead wood characteristics are no doubt the most 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 & Gafita 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 support 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; Norden 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 (Bitsan 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 36488 km² (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. 12122 km²) 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 m² 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 m², 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; Sem-Irlet 1995; Gerhardt 1999; Vasilyeva et al. 2007; Tănase et al. 2008; copoț et al., Lignicolous fungal assemblages in forests of the North-East Region, Romania)

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 $\beta$ clustering algorithm ($\beta = -0.25$) 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, Nematium 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 |
| *Plateus 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 capnoideus* (Fr.) P.Kumm. | 0.587 | 0.006 |
| *Mucidula mucida* (Schrad.) Pat. | 0.573 | 0.011 |
| *Chlorociboria* agg. | 0.568 | 0.018 |
| *Pluteus phlebophorus* (Ditmars) 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 episphearia* (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.) Wild. | 0.551 | 0.008 |
| *Peniophora quercina* (Pers.) Cooke | 0.530 | 0.04 |
| *Gymnopus fasicipes* (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* Boscau 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 lignicolous 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-
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 are 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*, *Tricholomopsis abietinum*). Many 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* Boșcai 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](image)

**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 (Kutszegi 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*, *Hyphenochaete 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 numularia* 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 macrofungi 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 (Copot 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 macrofungi 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 (Määkipää 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 areas. Less DCWD diversity might favour particular fungal species, known to grow on FWD, like *Fuscospora contigua*, *Vuilleminia comedens*, *Peniophora quercina*, *Lentinus arcurarius* (Bernicchia & Gorjón 2010) or on stumps, like *Panellus stipitatus*, *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 oaks. 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).

**Matutre 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 namus, P. umbrosus, Hypocrea gelatinosa, Flammulaster muricatus (Dvořák et al. 2017) or oak forests, as Oxyphorus 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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**REFERENCES**

Abrego N., Salcedo I. (2011) How does fungal diversity change based on woody debris type? A case study in Northern Spain. Ekologija 57(3): 109−119. https://doi.org/10.6001/ekologija.v57i3.1916

Abrego N., Halme P., Purhonen J., Ovaskainen O. (2016) Fruit body based inventories in wood-inhabiting fungi: Should we replicate in space or time? Fungal Ecology 20: 225−232. https://doi.org/10.1016/j.fuseno.2016.01.007

Andronache J., Fensholt R., Ahammer H., Ciobotaru A.-M., Pintili R.-D., Peptenatu D., Drăghici C.-C., Dacoum D.C., Raadulovic M., Pulighe G., Azihou A.F., Toyi M.S., Simin B. (2017) Assessment of textural differentiations in forest resources in Romania using fractal analysis. Forests 8(3): 54−74. https://doi.org/10.3390/f8030054

ANM – Administrația Națională de Meteorologie (2008) Clima României. București, Editura Academiei Române.

Bässler C., Müller J., Dziock F., Brandl R. (2010) Effects of resource availability and climate on the diversity of wood-decaying fungi. Journal of Ecology 98(4): 822−832. https://doi.org/10.1111/j.1365-2745.2010.01669.x

Bernicchia A., Gorjón S.P. (2010) Fungi Europaei - Corticiaceae s.l. Alessio, Edizioni Candusso.

Birsan C., Tănase C., Mardari C., Cojocariu A. (2014) Diversity and ecological determinants of dead wood fungi in tree natural reserves of broad leaved forests from Suceava county. Journal of Plant Development 21: 153−160.

Boddy L., Bardsley D.W., Gibbon O.M. (1987) Fungal communities in attached ash branches. New Phytologist 107(1): 143−154. https://doi.org/10.1111/j.1469-8137.1987.tb04888.x

Boddy L. (1993) Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. Mycological Research 97(6): 641−455. https://doi.org/10.1016/S0953-7562(09)80141-X

Bouriaud L. (2005) Causes of illegal logging in Central and Eastern Europe. Small-scale Forests Economics, Management and Policy 4(3): 269−292. https://doi.org/10.1007/s11842-005-0017-6

Breitenbach J., Kränzlin F. (1986) Champignons de Suisse. Tome 2. Champignons sans lames. Lucerne, Mykologia.

Brunet J., Fritz Ō., Richnau G. (2010) Biodiversity in European beech forests – a review with recommendations for suitable forest management. Ecological Bulletins 53: 77−94.

Cavender-Bares J., Izzo A., Robinson R., Lovelock C.E. (2009) Changes in ectomycorrhizal community structure on two containerized oak hosts across an experimental hydrologic gradi-
ent. Mycorrhizae. 19: 133–142. https://doi.org/10.1007/s00572-008-0220-3

Chifu T., Mânzu C., Zamfirescu O. (2006) Flora şi vegetaţia Moldovei (România). II Vegetaţia. Iaşi, Editura Universităţii Alexandru Ioan Cuza.

Conrad O., Bechtle B., Bock M., Dietrich H., Fischer E., Gerlitz L., Wehberg J., Wichmann V., Böhner J. (2015) System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geoscientific Model Development 8(1): 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Çolak A.H., Tokcan M., Kirca S. (2010) Dead Wood (Unseen Life on Dead). Istanbul, The Western Black Sea Forestry Research Institute.

Copot O., Balaq T., Birsan C., Petre C.V., Cojocariu A., Tănase C. (2018) Climatic predictors influence VFWD fungal diversity through dominant tree’ ecology in beech forests in the North-Eastern Romania. Journal of Plant Development 25: 119–134. https://doi.org/10.3362/jpd.2018.25.1.119

Courtecuisse R., Duhem B. (2013) Champignons de France et d’Europe. Paris, Delachaux et Niestlé.

Craibtree C.D., Keller H.W., Ely J.S. (2010) Macrofungi associated with vegetation and soils at Ha Ha Tonka State Park, Missouri. Mycologia 102(6): 1229–1239. https://doi.org/10.3852/08-138

De Cáceres M., Legendre P. (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90(12): 3566–3574. https://doi.org/10.1880/08-1823.1

Diyarova D.K. (2016) The role of wood-decaying fungi in the carbon cycle of forest ecosystems and the main ecological factors. European Scientific Journal, special edition: 162–166.

Dufrène M., Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67(3): 345–366. https://doi.org/10.2307/2963459

Dvořák D., Vašutová J., Hofmeister J., Beran M., Hošek J., Běťák J., Buré J., Deckerová H. (2017) Macrofungal diversity patterns in central European forests affirm the key importance of old-growth forests. Fungal Ecology 27: 145–154. https://doi.org/10.1016/j.fusco.2016.12.003

Ellis J.B., Everhart D.M. (1966) The North American Pyrenomycetes. A contribution to mycologic botany. New York, Johnson Reprint Corporation.

Eyssartier G., Roux P. (2013) Le guide des champignons. France et Europe. Paris, Belin.

Fick S.E., Hijmans R.J. (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302–4315. https://doi.org/10.1002/joc.5086

Frankland J.C., Hedger J.N., Swift M.J. (1982) Decomposer basidiomycetes: their biology and ecology. Cambridge, Cambridge University Press.

Führer E., Horváth L., Jagodics A., Machon A., Szabados I. (2011) Application of new aridity index in Hungarian forestry practice. Quarterly Journal of the Hungarian Meteorological Service 115(3): 205–216.

Gerhardt E. (1999) Guide Vigot des champignons. Paris, Vigot, Paris.

Gilbertson R.L., Ryvarden L. (1986) Abortiporus – Lindneria. In: North American Polypores, vol. 1. Oslo, Fungiflora.

Gilbertson R.L., Ryvarden L. (1987) Megaspororia – Wrightioporia. In: North American Polypores, vol. 2. Oslo, Fungiflora.

Goia I., Gaida D. (2018) Beech versus spruce deadwood as forest microhabitat: does it make any difference to bryophytes? Plant Biosystems 153(2): 187–194. https://doi.org/10.1080/11263504.2018.1448011

Halme P., Holec J., Heilmann-Clausen J. (2016) The history and future of fungi as biodiversity surrogates in forests. Fungal Ecology 27: 193–201. https://doi.org/10.1016/j.fusco.2016.10.005

Heilmann-Clausen J. (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycological Research 105(5): 575–596. https://doi.org/10.1017/S095375520103665

Heilmann-Clausen J., Christensen M. (2003) Fungal diversity on decaying beech logs - implications for sustainable forestry. Biodiversity and Conservation 12(5): 953–973. https://doi.org/10.1023/A:1022825809503

Heilmann-Clausen J., Aude E., Christensen M. (2005) Cryptogam communities on decaying deciduous wood – does tree species diversity matter? Biodiversity and Conservation 14(9): 2061–2078. https://doi.org/10.1007/s10531-004-4284-x

Heilmann-Clausen J., Aude E., van Dort K., Christensen M., Piltaväri A., Veerkamp M., Walleyn R., Siller I., Stanovárová T., Řodář P. (2014) Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – reflecting substrate quality or shaped by climate and forest conditions? Journal of Biogeography 41(12): 2269–2282. https://doi.org/10.1111/jbi.12388

Hennon P.E., Mulvey R.L. (2014) Managing heart rot in live trees for wildlife habitat in young-growth forests of Coastal Alaska. General Technical Report PNW-GTR-890, Portland, Department of Agriculture, Forest Service, Pacific Northwest Research Station, US. Available at https://www.fs.fed.us/pnw/pubs/pnwdtr890.pdf [accessed 23 Jan. 2020].

Holec J., Běťák J., Dvořák D., Křížková M., Kuchaříková M., Krzyziak-Kosińska R., Kučera T. (2019) Macrofungi on fallen oak trunks in the Białowieża Virgin Forest – ecological role of trunk parameters and surrounding vegetation. Czech Mycology 71(1): 65–89. https://doi.org/10.33585/cmy.71105

Hubert L., Arabie P. (1985) Comparing partitions. Journal of Classification 2: 193–218. https://doi.org/10.1007/BF01908075

Jančovičová S., Glejdura S. (1999) Ascomycetes from Danube islands in Bratislava (Slovakia). Tsaiszia – Journal of Botany 9: 1–10.

Jülich W. (1989) Aphyllophorales, Heterobasidiomycetes, Gasteromycetes. A contribution to mycologic botany. New York, Johnson Reprint Corporation.

Koide R.T., Fernandez C., Petprakob K. (2011) General principles in the community ecology of ectomycorrhizal fungi. Fungal Ecology 6: 1−10.

Kosińska R., Kučera T. (2019) Macrofungi on fallen oak trunks with vegetation and soils at Ha Ha Tonka State Park, Missouri. Ecological Monographs 89(1): 1−10.

Kubirowicz A., Angiolini C., Perini C., C., 2015: Concordance between vascular and groups of sites: indices and statistical inference. Biodiversity and Conservation 90(12): 3566–3574. https://doi.org/10.1007/s10531-004-4284-x

Koide R.T., Fernandez C., Petprakob K. (2011) General principles in the community ecology of ectomycorrhizal fungi. Annals of Forest Science 68: 45–55. https://doi.org/10.1007/s13595-010-0006-6

Kubartová A., Ranger J., Berthelin J., Beguiristain T. (2009) Diversity and decomposing ability of saprophytic fungi from temperate forest litter. Microbial Ecology 58(1): 98–107. https://doi.org/10.1007/s00248-008-9458-8

Küffer N., Gillet F., Senn-Irlet B., Aragno M., Job D. (2008) Ecological determinants of fungal diversity on dead wood in European forests. Fungal Diversity 30: 83–95.

Kutszegi G., Siller I., Dima B., Takács K., Merényi Z., Varga T., Turcsányi G., Bidlo A., Ődor P. (2015) Drivers of macrofungal species composition in temperate forests, West Hungary: functional groups compared. Fungal Ecology 17: 69–83. https://doi.org/10.1016/j.fusco.2015.05.009

Landi M., Salemi E., Ambrosio E., D’Aguanno M., Nucci A., Saveri C., Perini C., Angiolini C. (2015) Concordance between vascu-
lar plant and macrofungal community composition in broadleaf deciduous forests in central Italy. *iForest* 8(3): 279–286. https://doi.org/10.3832/ifor1199-008

Lifewatch (2019) LifeWatch-WB ecotope database. Available at http://lifewatch.bf/en/lifewatch-wb-ecotope-database [accessed 20 Feb. 2019].

Lombardi F., Cherubini P., Tognetti R., Coccozza C., Lasserre B., Marchetti M. (2013) Investigating biochemical processes to assess deadwood decay of beech and silver fir in Mediterranean mountain forests. *Annals of Forest Science* 70: 101–111. https://doi.org/10.1051/s13595-012-0230-3

Luchi N., Capretti P., Feducci M., Vannini A., Ceccarelli B., Vetraino A.M. (2015) Latent infection of *Biscogniauxia nummularia* in Fagus sylvatica: a possible bioindicator of beech health conditions. *iForest* 9(1): 49–54. https://doi.org/10.3832/ifor1436-008

Maechler M., Rousseeuw P., Struyf A., Hubert M., Hornik K. (2018) Cluster: Cluster Analysis Basics and Extensions. Available at https://svn.r-project.org/R-packages/trunk/cluster [accessed 23 Jan. 2022].

Mákipää R., Rajala T., Schigel D., Rinne K.T., Pennanen T., Abrego N., Ovaskainen O. (2017) Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. *The ISME Journal* 11: 1964–1974. https://doi.org/10.1038/ismej.2017.57

Mihál I., Blanár D. (2014) Fungi and slime molds of alder and willow alluvial forests of the upper part of the Muránka river (central Slovakia). *Folia Oecologica* 41(2):153–172.

Müller J., Engel H., Blaschke M. (2007) Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. *European Journal of Forest Research* 126: 513–527. https://doi.org/10.1007/s10342-007-0173-7

Neuwirth E. (2014) RColorBrewer: ColorBrewer Palettes. Available at https://CRAN.R-project.org/package=RColorBrewer [accessed 23 Jan. 2020].

Nordén B., Göttmark F., Tönberg M., Ryberg M. (2004) Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. *Forest Ecology and Management* 194(1–3): 235–248. https://doi.org/10.1016/j.foreco.2004.02.043

Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O’Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E., Wagner H. (2018) vegan: Community Ecology Package. Available at https://cran.r-project.org/package=vegan [accessed 23 Jan. 2020].

Packham J.M., May T.W., Brown M.J., Wardlaw T.J., Mills A.K. (2002) Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: a multivariate study. *Austral Ecology* 27(2): 149–161. https://doi.org/10.1046/j.1442-9993.2002.01167.x

Petre C.V., Balaș T., Tănase C. (2014) Lignicolous basidiomycetes as valuable biotechnological agents. *Memoirs of the Scientific Sections of the Romanian Academy. Biology* 37: 37–62.

Pouška V., Macek P., Zíharová L. (2016) The relation of fungal communities to wood microclimate in a mountain spruce forest. *Fungal ecology* 21: 1–9. https://doi.org/10.1016/j.fungeco.2016.01.006

Purhonen J., Huhtinen S., Kotiranta H., Kotiaho J.S., Halmi P. (2017) Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection. *Fungal Ecology* 27: 175–177. https://doi.org/10.1016/j.fungeco.2016.06.007

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.r-project.org/ [accessed 23 Jan. 2020].

Raja H.A., Miller A.N., Pearce C.J., Oberlies N.H. (2017) Fungal identification using molecular tools: a primer for the natural products research community. *Journal of Natural Products* 80(3): 756–770. https://doi.org/10.1021/acs.jnatprod.6b01085

Rand W.M. (1971) Objective criteria for the evaluation of clustering methods. *Journal of the American Statistical Association* 66: 846–850. https://doi.org/10.2307/2284239

Rudolf K., Morschhauser T., Pál-Fám F. (2012) Macrofungal diversity in disturbed vegetation types in North-East Hungary. *Central European Journal of Biology* 7(4): 634–647. https://doi.org/10.2478/s11535-012-0050-3

Runnel K., Löhmus A. (2017) Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. *Fungal Ecology* 27: 155–167. https://doi.org/10.1016/j.fungeco.2016.09.006

Ryvarden L. (1976) Albatrellus – Incrustoporia. In: Ryvarden L. (ed.) The Polyporaceae of North Europe, vol. 1. Oslo, Fungiflora.

Ryvarden L. (1991) Genera of Polypores. Nomenclature and taxonomy. Synopsis Fungorum, vol. 5. Oslo, Fungiflora.

Ryvarden L., Gilbertson R.L. (1994) European Polypores. Part 2. Meripilus – Tyromyces. In: Ryvarden L., Gilbertson R.L. (eds) Synopsis Fungorum, vol 7. Oslo, Fungiflora.

Sefidi K., Darabad F.E., Azaryan M. (2016) Effect of topography on tree species composition and volume of coarse woody debris in an Oriental beech (*Fagus orientalis* Lipsky) old growth forests, northern Iran. *iForest – Biogeosciences and Forestry* 9(4): 658–665. https://doi.org/10.3832/ifor1080-008

Semi-Inlet B. (1995) The genus *Crepidotus* (Fr.) Staude in Europe. *Persoonia* 16(1): 1–80.

Stasińska M. (2008) Contribution to chorology of *Xylobolus frutulatus* in Poland. *Acta Mycologica* 43(2): 167–171. https://doi.org/10.5586/am.2008.021

Tavankar F., Picchio R., Lo Monaco A., Bonyad A.E. (2014) Forest management and snag characteristics in Northern Iran lowland forests. *Journal of Forest Science* 60(10): 431–441. https://doi.org/10.17221/77/2014-JFS

Tânase C., Pop A. (2005) Lista Roșie a Macromicetelor din România. Bioplatform – Romanian National Platform for Biodiversity. București, Editura Academiei Române.

Tânase C., Birsan C., Chiricoiu A., Cociocariu A. (2009) Macromycete from Romania. Iași, Editura Universității Alexandru Ioan Cuza.

Vasilyeva L.N., Rogers J.D., Miller A.N. (2007) Pyrenomycetes of *Picea glauca* (Pinaceae). *Persoonia* 52(2): 658−665. https://doi.org/10.3832/ifor1080-008

Wairiu K., Lõhmus A. (2017) Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. *Fungal Ecology* 27: 155–167. https://doi.org/10.1016/j.fungeco.2016.09.006

Wickham H. (2007) Reshaping data with the reshape Package. *Journal of Statistical Software* 21(12): 1–20. https://doi.org/10.18637/jss.v021.i12
Wickham H. (2016) ggplot2: elegant graphics for data analysis. 2nd Edition. New York, Springer-Verlag. [https://doi.org/10.1007/978-3-319-24277-4](https://doi.org/10.1007/978-3-319-24277-4)

Zabel R.A., Morrell J.J. (1992) Wood microbiology: decay and its prevention. San Diego, Academic Press.

Županić M., Matošević D., Pernek M., Diminić D. (2009) Lignicolous fungi on Pedunculate oak in lowland forests of Central Croatia. *Periodicum Biologorum* 111(4): 397–403.

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