



Structure of fungal communities (Ascomycota, Basidiomycota) in Western Carpathian submontane forest stands under different managements

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Abstract

In our paper, we present a mycocoenological study of two, differently managed beech forest stands (a 28year-old pole-sapling stand – plot H and a control 115yearold mature stand – plot K) in temperate forests of The Western Carpathians. Out of 117 identified species of macromycetes, 87 species were found at plot H and 72 species at plot K. Altogether, 63% of fruiting bodies abundance was recorded at plot H and 37% was recorded at plot K. Together, 41 species (35.04%) had a common occurrence at both plots. We found 55 wood-inhabiting species, of which the most abundant production of fruiting bodies were by species *Panellus stipticus* (797 fruiting bodies), *Hypoxylon fragiforme* (480), *Lycoperdon pyriforme* (408); 32 ectomycorrhizal species, with the largest production of fruiting bodies by *Craterellus cornucopioides* (94 fruiting bodies), *Russula foetens* (36), *Lactarius piperatus* (24); and 27 species of terrestrial saprotrophs, out of which the most fruiting bodies were produced by species *Mycena alcalina* agg. (52 fruiting bodies), *Mycena inclinata* (50), *Psathyrella laevissima* (38). At plot K, the values of overall biomass production of fruiting bodies, as well as biomass of fruiting bodies of ectomycorrhizal species, were higher compared to plot H.

Key words – abundance of sporocarps – beech – biomass production – *Fagus sylvatica* L. – macrofungi – managed forests

Introduction

European beech (*Fagus sylvatica* L.) is an important tree species due to high representation in the forests of Slovakia and throughout Central Europe. Beech, which presently covers 31.4% of the total forest land in Slovakia, was the leading woody plant in the country in the year 2008 (Barna et al. 2011).

Macromycetes growing in beech forest stands build an intricate ecotrophic–ecotopic system linked with beech and with the beech-associated environment. Mihál (2012a) notes that each fungal community in beech stands is characterised by its species diversity and dominance, abundance, distribution and fruiting bodies production of individual fungal species. Various disturbances in forest environment change the overall structure of trees, plants and microclimates of forest stands which consequently shows also in the structure of fungal communities. Similarly, the effects of

forest fragmentation on a wood-inhabiting fungal community in beech forest stands are assessed by Abrego & Salceda (2014) in northern Spain. Abrego et al. (2017) studied how environmental drivers influence the occurrence of wood-inhabiting macro-fungi in European beech forests.

Soil conditions are of great importance for the occurrence, spread and structure of in forest stands. For example, in the case of beech forest stands, Gryndler et al. (2004) state that fructification and fruiting body production of ectomycorrhizal macromycetes are fundamentally influenced by the quality of the forest stand, i.e. herbal cover and soil condition. According to Holec (1994), litter thickness and humus form influence the numbers of saprotrophic and ectomycorrhizal fungi and their ratio.

Human interference with forest environment often negatively alters microclimatic conditions of affected stands. A common phenomenon in such stands is the growth of dead or dying woody substrate left after harvests which is successively occupied by wood-inhabiting fungi. A similar situation occurs in beech forests after logging when the open areas change microclimatic conditions, e.g. increased insolubility, soil desiccation and the process of secondary succession – weed infestation (Mihál 1994, 1995). Kutszegi et al. (2015) say that wood-inhabiting fungal species composition is driven primarily by the species composition of living trees, while substrate properties and microclimate play minor roles. Baldrian et al. (2016) indicate that the amount of deadwood represents a very diverse substrate in terms of quality and quantity of fungal biomass as well as the species diversity of fungal communities.

Perhaps the most notable manifestation of the disturbance of forest stands is changes in species diversity and productivity of symbiotic – ectomycorrhizal species of fungi, which also affects the health status of forest trees. Mycorrhiza is a symbiotic association of fungi with the roots of plants. As much as 30 – 35% of energy gained by a beech forest via photosynthesis is metabolized by mycorrhizal fungi (Jennings & Lysek 1996). Communities of symbiotic fungi are heavily dependent on sufficient density, accessibility and variety of forest trees, but also on certain ratios of biogenic chemical elements in the soil. For example, the importance of phosphorus as an element supporting the abundance and overall structure of symbiotic fungi community is emphasized by Burke et al. (2009). The influence of different concentrations of Ca, K, P, Mg and Fe on species diversity of ectomycorrhizal fungi is reported by Lang & Polle (2011). According to Suz et al. (2015) the N pollution and soil pH are emerging as major factors driving ectomycorrhizal communities through impacts on tree roots, fungi, and soil conditions.

The problems of productivity and production of epigeic sporocarps of symbiotic fungi were mentioned by Bonet et al. (2004) who studied the relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi. Interdependence of thinning in beech stands and productivity of macromycetes is reported by Egli et al. (2010).

In our paper, we present the results of studies from two differently managed submontane beech stands (28-year-old pole-sapling stand and 115-year-old mature stem control stand) in temperate forests of the Western Carpathians. For our working hypothesis, we assumed greater species diversity and productivity of wood-inhabiting macromycetes and ectomycorrhizal symbionts in the coppice stand versus the stand of mature stems on the basis of different ecotopic and ecotrophic conditions at both localities (e.g. richer species diversity of trees and larger amount of woody substrate in coppice stand).

Materials & Methods

Characteristics of localities

Mycological research was carried out in 2015 and 2016 in submontane beech stands at the Ecological Experimental Station (EES) Kováčová (Central Slovakia, Western Carpathians). Two sites were selected as research plots: plot H where a whole area clear-fell was carried out in 1989 and presently the succession stand is in the pole-stage sapling (Fig. 1); and plot K which represents a control stand of mature stems with no harvesting interference (Fig. 2). At each plot, mycological research was carried out in the stand within an area of 100 m². Basic characteristics of the two plots

are shown in Table 1. More specific description, characteristics and selected soil, climatic, forestry and ecological conditions of the EES Kováčová station are described by Barna & Bošela (2015) and Schieber et al. (2015).

Table 1 Characteristics of research plots (H and K) in the Ecological-Experimental Station (EES) Kováčová.

Characteristics	H	K
Geographic coordinates	48° 38' N, 19° 04' E	48° 38' N, 19° 04' E
Size (ha)	0.40	0.40
Aspect	SW	SW
Prevailing wind direction	NW	NW
Altitude (m a.s.l.)	480 – 510	480 – 510
Slope (°)	5 – 15	5 – 15
Geological substrate	andesite, tuffits agglomerates	andesite, tuffits agglomerates
Soil	cambisol modal, saturated	cambisol modal, saturated
pH (H ₂ O)	5.44	5.61
Mean annual precipitation (mm)	780	780
Mean annual temperature (°C)	6.8	6.8
Forest type	<i>Fagetum pauper inferiora</i>	<i>Fagetum pauper inferiora</i>
Plant association	<i>Dentario bulbiferae- Fagetum</i> , <i>Carici pilosae- Fagetum</i>	<i>Dentario bulbiferae- Fagetum</i> , <i>Carici pilosae- Fagetum</i>
Age of stand (years)	28	115
Growth phase of stand	pole stage stand	mature stand (control plot)
Stocking	1.0	1.0
Crown cover (%)	97	97
Tree species composition (%)	hornbeam 44, lime 37, beech 12, aspen 5, acer 1, oak 1	beech 96, fir 4
Content of C in soil (%) *	3.64	4.93
Content of K in soil (mg.kg) *	175	230
Content of humus (%) *	6.3	8.5

*The content of selected chemical components and humus is given by Stašiov (2002).

Methods of research

Mycological research in predominantly beech forests of both plots (H and K) at the EES Kováčová took place once a month from May to November during the growing seasons in 2015 and 2016. The species diversity of macromycetes was documented and identified in the field or in the laboratory. Abundance (number of sporocarps – A) and distribution (number of occurring places of sporocarps – D) were recorded and the value of dominance of each species (Do) was given by $A + D = Do$. The values of sporocarps biomass production of selected macromycetes were calculated by average weight of one exemplar of sporocarps multiplied by total abundance of evaluated species. We present the biomass of fresh weight of sporocarps (kg.ha⁻¹).

To assess the syntaxony, species diversity was divided into two basic ecotrophic groups: 1. wood-inhabiting species (parasitic and saprotrophs) growing only on woody substrate; 2. Terrestrial species (ectomycorrhizal and saprotrophs) growing from soil and debris. Mycoparasitic and herboparasitic fungi were also recorded. Assessing the importance of mycorrhizal macromycetes, we also present the values of ectomycorrhizal potential (MPo) and mycorrhizal percentage (MPe). These were respectively calculated as a ratio of the number of mycorrhizal species and the number of terrestrial saprophytic species (MPo) and as a ratio of the number of mycorrhizal species and the number of all identified macromycetes (MPe) (cf. Gáper & Mihál 2008, Gulden et al. 1992). These procedures are described in detail by Mihál (1995, 2012a, b) and Mihál & Bučinová (2005, 2007).



Figure 1 – A view of the 28-year-old forest stand at plot H (pole stage stand), photo: E. Luptáková.



Figure 2 – A view of the 115-year-old forest stand at control plot K (mature stand), photo: B. Schieber.

Selected specimens are deposited in the private herbarium of the senior author at the Institute of Forest Ecology, Slovak Academy of Sciences in Zvolen. The scientific nomenclature of macromycetes species is given by Cooper & Kirk (2017), Škubla (2003).

Statistical analysis

Species abundance data were collected during the period from May to November in 2015 and 2016. Samples from sites K and H were obtained monthly by surveying a randomly chosen area of 100 m² at each site. 7 samples were collected from each plot each year resulting in a total of 28 samples. The species abundance data were divided into three species groups of fungi representing wood-inhabiting, mycorrhizal, and other fungi species. The three fungal groups were processed separately in all analyses.

The effects of site and season on the wood-inhabiting group were tested by permutational multivariate analysis of variance (perMANOVA, Anderson 2001) on Bray–Curtis distances (Bray & Curtis 1957) calculated from $\log(x+1)$ transformed species abundance data. The test was carried out using unrestricted permutation of residuals with 9,999 random permutations. Mycorrhizal and other terrestrial saprotrophic fungi species were not analysed by perMANOVA due to too many zero samples in the species abundance data. Results of the two-way perMANOVA wood-inhabiting species model are presented by non-metric multidimensional scaling (NMDS, Kruskal 1964). After several random starts, final NMDS solution was centred and rotated so that the first NMDS axis represents the largest variance of points. Half-change scaling was used to scale the solution so that one unit in NMDS ordination space corresponds to halving the community similarity. The stress method was used to assess interpretation reliability of distances between points in ordination.

Association between the two sites and species of the wood-inhabiting group was tested by analysis of indicator species using IndVal function (Dufrêne & Legendre 1997) and 9,999 permutations. Results of the indicator species analysis were adjusted for multiple testing using Holm's method (Holm 1979).

Abundance, species richness and Shannon index of diversity (natural logarithm) of the wood-inhabiting, mycorrhizal and other terrestrial saprotrophic fungi species were analysed by specific two-way ANOVA-like models. Negative binomial models (NB) with log-link were used to test the effect of site and season on the abundance of the three fungal species groups. Poisson models (GLMp) with log-link were used to test the effect of site and season on species richness. Linear models (LM) were used to test the effect of site and season on Shannon index of diversity. LM was also used to test the two factors on the production of selected species. Tests were done using PIT-trap re-sampling method (Warton et al. 2017) which bootstraps (9,999) probability integral transform residuals and gives the most reliable Type I error rates. Results of the two-way ANOVA like models were graphically displayed using bar plots. Means of all 4 combinations of the site and the season along with 95% non-parametric bootstrap (9,999) confidence intervals using the bias-corrected and accelerated percentile method (Efron & Tibshirani 1986) were used in the bar plots. Level of significance was $p=0.05$ and only significant results are interpreted in figures.

All statistical analyses and graphics were done in R (R Core Team 2016) using packages boot (Canty & Ripley 2016), indicpecies (De Cáceres & Legendre 2009), mvabund (Wang et al. 2017) and vegan (Oksanen et al. 2017).

Results

Wood-inhabiting fungi

The macromycetes species spectrum, ecotrophic selection, and relative fruiting bodies abundance (A/%) within individual plots (H and K) during the investigated period are given in Table 2. Table 2 shows that from the total number of 117 identified macromycetes species, 87 species were recorded at plot H and 72 species were recorded at plot K. Similarly, up to 63% of the total abundance of macromycetes fruiting bodies was recorded at plot H, while plot K contained 37% of the total abundance of fruiting bodies. 41 species of macromycetes (35.04%) occurred commonly at both plots. Out of a total of 117 identified species of macromycetes, there were 55 wood-inhabiting species, some of which produced the largest quantities of fruiting bodies (e.g. *Panellus stipticus* (797 fruiting bodies), *Hypoxylon fragiforme* (480), *Lycoperdon pyriforme* (408).

Table 2 Macromycetes species spectrum, ecotrophical selection and relative fruiting body abundance (A/%) within individual plots (H and K) during investigated period.

Species	EG	H: A/%	K: A/%
<i>A s c o m y c o t a</i>			
* <i>Aleuria aurantia</i> (Pers.) Fuckel	TS	14/0.50	
<i>Annulohypoxylon multifforme</i> (Fr.) Y. M. Ju, J. D. Rogers & H. M. Hsieh	WS	28/1.0	49/2.97
<i>Ascodichaena rugosa</i> Butin	LS	18/0.64	140/8.49
<i>Biscogniauxia nummularia</i> (Bull.) Kuntze	WP		17/1.03
<i>Bisporella citrina</i> (Batsch) Korf & S. E. Carp.	WS	14/0.50	
<i>Cytospora populina</i> (Pers.) Rabenh.	WS	10/0.36	10/0.61
<i>Diatrype disciformis</i> (Hoffm.) Fr.	WS	172/6.14	176/10.68
<i>Eutypella quaternata</i> (Pers.) Rappaz	WS	204/7.28	202/12.26
<i>Helvella pezizoides</i> Afzel	TS	1/0.03	
<i>Humaria hemisphaerica</i> (F. H. Wigg.) Fuckel	EM	1/0.03	
<i>Hypomyces chrysospermus</i> Tul. & C. Tul.	MP	18/0.64	10/0.61
<i>Hypoxylon fragiforme</i> (Pers.) J. Kickx f.	WS	299/10.67	181/10.98

Table 2 Continued.

Species	EG	H: A/%	K: A/%
<i>Kretzschmaria deusta</i> (Hoffm.) P. M. D. Martin	WS	96/3.42	
* <i>Leotia lubrica</i> (Scop.) Pers.	TS		1/0.06
<i>Melanopsamma pomiformis</i> (Pers.) Sacc.	WS		23/1.36
<i>Nectria cinnabarina</i> (Tode) Fr.	WS	3/1.39	
* <i>Peziza arvernensis</i> Boud.	TS		1/0.06
<i>Pseudovalsa spinifera</i> (Wallr.) M. E. Barr	WS	28/1.0	6/0.36
<i>Rhytisma acerinum</i> (Pers.) Fr.	HP	59/2.10	16/0.97
<i>Valsa ambiens</i> (Pers.) Fr.	WS		12/0.73
<i>Xylaria hypoxylon</i> (L.) Grev.	WS	15/0.53	
B a s i d i o m y c o t a			
* <i>Amanita vaginata</i> (Bull.) Lam.	EM	2/0.07	
* <i>Ampulloclitocybe clavipes</i> (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	TS		1/0.06
<i>Artomyces pyxidatus</i> (Pers.) Jülich	WS	5/0.18	
<i>Bjerkandera adusta</i> (Willd.) P. Karst.	WS	7/0.25	
<i>Botryobasidium laeve</i> (J. Erikss.) Parmasto	WS		4/0.24
* <i>Cantharellus cibarius</i> Fr.	EM		1/0.06
* <i>Cerioporus varius</i> (Pers.) Zmitr. & Kovalenko	WS	1/0.03	13/0.79
<i>Chondrostereum purpureum</i> (Pers.) Pouzar	WS	28/1.0	
<i>Clavariadelphus pistillaris</i> (L.) Donk	EM		1/0.06
<i>Clitopilus scyphoides</i> (Fr.) Singer	TS	1/0.03	
* <i>Coprinellus domesticus</i> (Bolton) Vilgalys, Hoppe & Jacq. Johnson	TS	1/0.03	
* <i>C. micaceus</i> (Bull.) Vilgalys, Hopple & Jacq. Johnson	TS		1/0.06
* <i>Cortinarius multififormis</i> Fr.	EM		2/0.12
* <i>C. turmalis</i> Fr.	EM	4/0.14	6/0.36
* <i>C. vernus</i> H. Lindstr. & Melot	EM	5/0.18	
* <i>Craterellus cornucopioides</i> (L.) Pers.	EM	7/0.25	87/5.28
<i>Daedaleopsis confragosa</i> (Bolton) J. Schröt.	WS	3/1.39	3/0.18
<i>Exidia glandulosa</i> (Bull.) Fr.	WS	26/0.93	18/1.09
<i>Ganoderma orbiforme</i> (Fr.) Ryvarden	WS	7/0.25	
* <i>Galerina hypnorum</i> (Schränk) Kühner	WS	2/0.07	
* <i>G. marginata</i> (Batsch) Kühner	WS	1/0.03	
* <i>Gymnopus confluens</i> (Pers.) Antonín, Halling & Noordel.	TS	25/0.89	
* <i>G. erythropus</i> (Pers.) Antonín, Halling & Noordel.	TS	5/0.18	2/0.12
* <i>G. foetidus</i> (Sowerby) P. M. Kirk	LS	8/0.28	221/13.41
* <i>G. fusipes</i> (Bull.) Gray	WP	5/0.18	
* <i>G. peronatus</i> (Bolton) Gray	TS		9/0.55
* <i>Hebeloma sinapizans</i> (Paulet) Gillet	EM	4/0.14	
* <i>Hydropus subalpinus</i> (Höhn.) Singer	TS		3/0.18
* <i>Hygrophorus eburneus</i> (Bull.) Fr.	EM	1/0.03	1/0.06
* <i>Hymenopellis radicata</i> (Relhan) R. H. Petersen	WS	19/0.68	1/0.06
* <i>Hypholoma fasciculare</i> (Huds.) P. Kumm.	WS		52/3.15
* <i>H. lateritium</i> (Schaeff.) P. Kumm.	WS	53/1.89	
* <i>Inocybe asterospora</i> Quél.	EM	4/0.14	1/0.06
<i>Irpex lacteus</i> (Fr.) Fr.	WS		4/0.24
* <i>Laccaria laccata</i> agg.	EM	3/0.11	
* <i>Lactarius blennius</i> (Fr.) Fr.	EM	7/0.25	2/0.12
* <i>L. pallidus</i> Fr.	EM	4/0.14	27/1.64
* <i>L. piperatus</i> (L.) Pers.	EM	13/0.46	11/0.67
* <i>L. subdulcis</i> (Pers.) Gray	EM	1/0.03	1/0.06
* <i>Leccinum aurantiacum</i> (Bull.) Gray	EM	2/0.07	
* <i>L. scabrum</i> (Bull.) Gray	EM	18/0.64	
<i>Lenzites betulina</i> (L.) Fr.	WS	32/1.14	

Table 2 Continued.

Species	EG	H: A/%	K: A/%
<i>*Lycoperdon lividum</i> Pers.	TS	3/0.11	
<i>*L. pyriforme</i> Schaeff.	WS	349/12.45	59/3.58
<i>*L. utriforme</i> Bull.	TS		7/0.42
<i>*Megacollybia platyphylla</i> (Pers.) Kotl. & Pouzar	WS	10/0.36	2/0.12
<i>*Mycena alcalina</i> agg.	TS	16/0.57	36/2.18
<i>*M. capillaris</i> (Schumach.) P. Kumm.	TS	1/0.03	
<i>*M. crocata</i> (Sched.) P. Kumm.	TS	3/0.11	
<i>*M. filipes</i> (Bull.) P. Kumm.	TS		2/0.12
<i>*M. galericulata</i> (Scop.) Gray	WS	3/0.11	
<i>*M. haematopus</i> (Pers.) P. Kumm.	TS		9/0.55
<i>*M. inclinata</i> (Fr.) Quél.	TS	50/1.78	
<i>*M. polygramma</i> (Bull.) Gray	TS	1/0.03	
<i>*M. pura</i> (Pers.) P. Kumm.	TS	3/0.11	3/0.18
<i>*M. renati</i> Quél.	WS	37/1.32	24/1.46
<i>*M. stylobates</i> (Pers.) P. Kumm.	TS	1/0.03	6/0.36
<i>*Mycetinis alliaceus</i> (Jacq.) Earle ex A. W. Wilson & Desjardin	WS	8/0.28	7/0.42
<i>*Oudemansiella melanotricha</i> (Dörffelt) M. M. Moser	WS	1/0.03	
<i>*Panellus stipticus</i> (Bull.) P. Karst.	WS	797/28.43	
<i>Peniophora incarnata</i> (Pers.) P. Karst.	WS		3/0.18
<i>Phanerochaete laevis</i> (Fr.) J. Erikss. & Ryvarden	WS	72/2.57	4/0.24
<i>*Pleurotus pulmonarius</i> (Fr.) Quél.	WP		1/0.06
<i>Postia fragilis</i> (Fr.) Jülich	WS		6/0.36
<i>*Pluteus cervinus</i> (Schaeff.) P. Kumm.	WS	4/0.14	3/0.18
<i>*P. nanus</i> (Pers.) P. Kumm.	WS	1/0.03	
<i>*Polyporus arcularius</i> (Batsch) Fr.	WS	1/0.03	
<i>*Psathyrella candolleana</i> (Fr.) Maire	TS	14/0.50	
<i>*P. laevissima</i> (Romagn.) Singer	TS	35/1.25	3/0.18
<i>*Psilocybe crobula</i> (Fr.) Singer	WS	1/0.03	
<i>Ramaria largentii</i> Marr. & D. E. Stuntz	EM		1/0.06
<i>R. stricta</i> (Pers.) Quél.	EM		2/0.12
<i>Resinicium bicolor</i> (Alb. et Schwein.) Parmasto	WS	6/0.21	
<i>*Russula claroflava</i> Grove	EM	1/0.03	
<i>*R. cyanoxantha</i> (Schaeff.) Fr.	EM	12/0.43	11/0.67
<i>*R. faginea</i> Romagn. ex Romagn.	EM	1/0.03	1/0.06
<i>*R. fellea</i> (Fr.) Fr.	EM	4/0.14	5/0.30
<i>*R. foetens</i> Pers.	EM	8/0.28	28/1.34
<i>*R. heterophylla</i> (Fr.) Fr.	EM		4/0.24
<i>*R. nigricans</i> Fr.	EM	8/0.28	2/0.12
<i>*R. nobilis</i> Velen.	EM		1/0.06
<i>*R. vesca</i> Fr.	EM	1/0.03	
<i>*R. virescens</i> (Schaeff.) Fr.	EM	1/0.03	
<i>Schizophyllum commune</i> Fr.	WS	12/0.43	1/0.06
<i>Stereum rugosum</i> Pers.	WP		3/0.18
<i>S. hirsutum</i> (Willd.) Pers.	WS	20/0.71	68/4.13
<i>*Stropharia aeruginosa</i> (Curtis) Quél.	WS	13/0.46	2/0.12
<i>Trametes gibbosa</i> (Pers.) Fr.	WS	5/0.18	
<i>T. hirsuta</i> (Wulfen) Lloyd	WS		3/0.18
<i>T. versicolor</i> (L.) Lloyd	WS	6/0.21	15/0.91
<i>Trichaptum abietinum</i> (Dicks.) Ryvarden	WS		4/0.24
<i>*Tricholoma album</i> (Schaeff.) P. Kumm.	EM	1/0.03	
<i>*T. sejunctum</i> (Sowerby) Quél.	WS		1/0.06
<i>*Tubaria furfuracea</i> (Pers.) Gillet	TS	8/0.28	
<i>*Typhula fistulosa</i> (Holmsk.) Olariaga	TS	1/0.03	

Table 2 Continued.

Species	EG	H: A/%	K: A/%
<i>*Xerocomellus chrysenteron</i> (Bull.) Šutara	EM		1/0.06
Abundance of total number /%		2,803/63.0	1,648/37.0
Abundance of total number (H+K) /%		4,451/100.0	

EG: ecotrophic groups: WP: wood-inhabiting parasites, HP: herboparasites, MP: mycoparasites, WS: wood-inhabiting saprotrophs, TS: terrestrial saprotrophs, EM: ectomycorrhizal symbionts, * – species for evaluation of biomass production

The species groups of wood-inhabiting fungi were significantly shaped mainly by the effect of site (Table 3). The effect of season on composition of the groups was also significant, but it was driven by a stronger effect of site resulting in significant interaction (Table 3, Fig. 3). Of 56 wood-inhabiting fungi species, 10 were significantly associated with one of the two sites after p values were adjusted for multiple testing (Table 4). The abundance of wood-inhabiting fungi was significantly higher at site H (Fig. 4), but the effect of season was not significant (Table 5). Species richness was also significantly higher at site H (Fig. 5) and the season was not significant (Table 5). Shannon diversity index was not affected by any of the two factors (Table 5).

Table 3 Results of perMANOVA on Bray–Curtis distances for assemblages of wood-inhabiting fungi surveyed on sites K and H in the seasons 2015 and 2016 from the EES Kováčová stand. P values are based on the specific resampling method (see methods).

Source	pseudo-F	P
Site	57.179	0.0001
Season	13.588	0.0001
Site x Season	6.237	0.0036

Table 4 Results of indicator species analysis (IndVal) on the wood-inhabiting species abundance data surveyed at sites K and H during the two seasons from the EES Kováčová stand. Displayed are species which had statistically significant association to one of the two sites after adjustment of p values for multiple testing by Holm's method.

Species	Site	IndVal	p	Species	Site	IndVal	P
AscoRugo	K	0.89	0.001	PhanLeav	H	0.95	0.001
SterHirs	K	0.77	0.001	XylaHypo	H	0.86	0.001
KretDeus	H	1.00	0.001	PseuSpin	H	0.82	0.001
ChondPurp	H	1.00	0.001	HypoFrag	H	0.62	0.001
LenzBetu	H	1.00	0.001				
PaneStip	H	1.00	0.001				

AscoRugo – *Ascodichaena rugosa*, SterHirs – *Stereum hirsutum*, KretDeus – *Kretzschmaria deusta*, ChondPurp – *Chondrostereum purpureum*, LenzBetu – *Lenzites betulina*, PaneStip – *Panellus stipticus*, PhanLeav – *Phanerochaete laevis*, XylaHypo – *Xylaria hypoxylon*, PseuSpin – *Pseudovalsa spinifera*, HypoFrag – *Hypoxylon fragiforme*

Table 5 Results of two-way ANOVA-like negative binomial (NB), poisson (GLMp) and linear models (LM) of wood-inhabiting fungi abundance, species richness and Shannon index of diversity of the sites K and H in the seasons 2015 and 2016 from the EES Kováčová stand. P values are based on the specific resampling method (see methods).

Type of model/Source	Test statistic	P
NB Abundance	Deviance	
Site	14.54	<0.0001
Season	0.16	0.72
Site x Season	1.04	0.37
GLMp Species richness	Deviance	
Site	12.82	<0.0001
Season	0.25	0.68
Site x Season	0.34	0.30
LM Shannon index	F	
Site	0.08	0.78
Season	0.61	0.44
Site x Season	0.48	0.49

Ectomycorrhizal fungi

The abundance of ectomycorrhizal fungi was affected by season - it was significantly higher in 2016 (Fig. 6). The effect of the site on abundance was not significant (Table 6). Species richness was also significantly higher in 2016 (Fig. 7), but it was not affected by site (Table 6). Shannon diversity index was not significantly different between plots K and H in the season of 2016. Of the total number of 117 identified species of macromycetes (Table 2), there were 32 ectomycorrhizal species of which the most fruiting bodies were produced by *Craterellus cornucopioides* (94 fruiting bodies), *Russula foetes* (36) *Lactarius piperatus* (24).

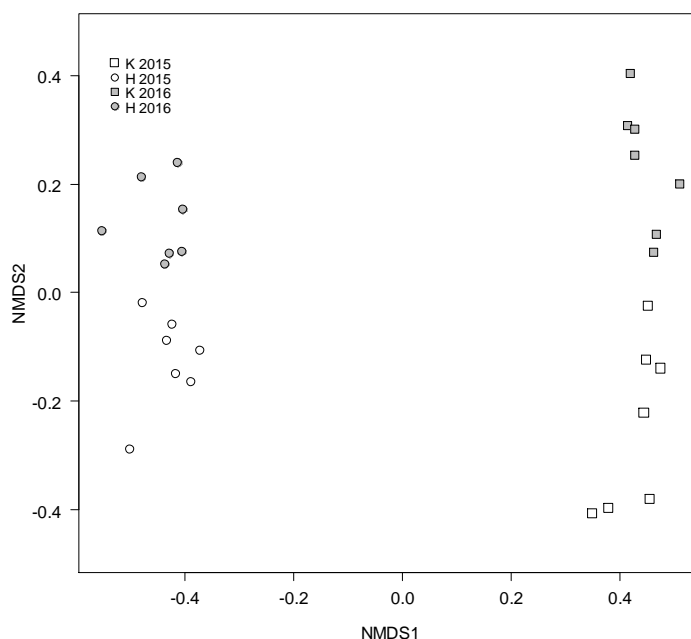


Figure 3 – Non-metric multidimensional scaling on Bray-Curtis distances for wood-inhabiting fungi assemblages surveyed at sites K and H in seasons 2015 and 2016 from the EES Kováčová stand. NMDS1 axis represents the largest variance of the points. One unit in NMDS ordination space corresponds to halving of assemblage similarity. Stress = 0.086.

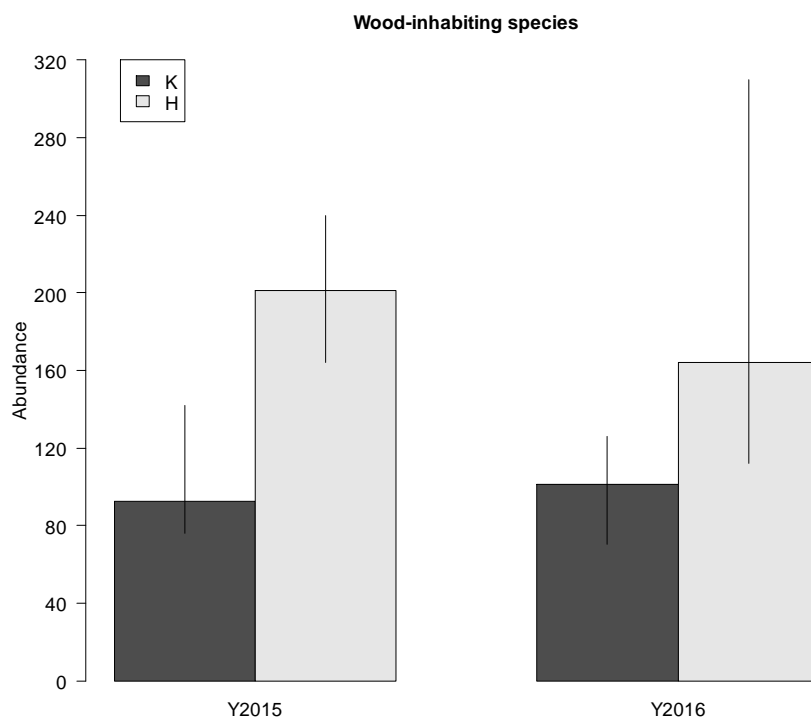


Figure 4 – Mean abundance of wood-inhabiting fungi for 100 m² at sites K and H during seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

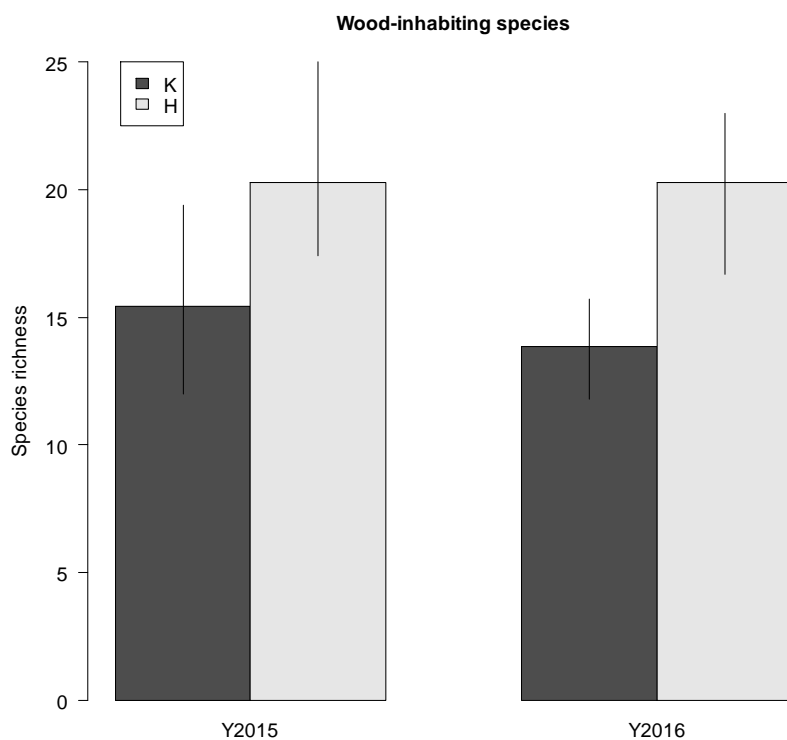


Figure 5 – Mean species richness of wood-inhabiting fungi for 100 m² at sites K and H during seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

Table 6 Results of two-way ANOVA like negative binomial (NB), poisson (GLMp) and linear models (LM) of ectomycorrhizal fungi abundance, species richness and Shannon index of diversity of sites K and H in seasons 2015 and 2016 from the EES Kováčová stand. Shannon index was analysed only in season 2016 as the result of too many zero samples in season 2015. P values are based on the specific resampling method (see methods).

Type of model/Source	Test statistic	P
NB Abundance	Deviance	
Site	0.47	0.52
Season	14.34	<0.0001
Site x Season	0.09	0.74
GLMp Species richness	Deviance	
Site	0.01	0.91
Season	13.70	0.001
Site x Season	0.15	0.72
LM Shannon index	F	
Site	0.004	0.95

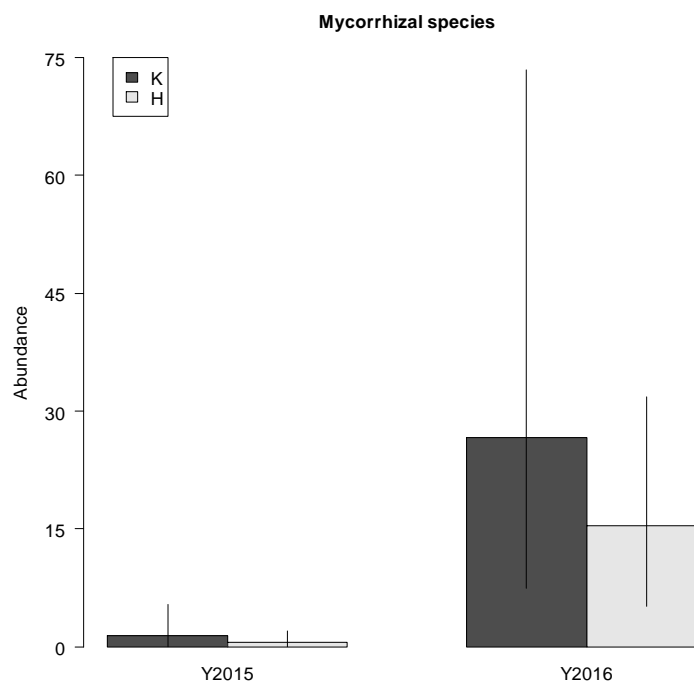


Figure 6 – Mean abundance of mycorrhizal fungi for 100 m² at sites K and H during seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

The values of mycorrhizal potential (MPo) and mycorrhizal percentage (MPe) at individual subplots were as follows: at plot H, the MPo value was 1.98 and the MPe value was 27.1; whereas at plot K, the MPo value was 1.29 and the MPe value was 26.4. Higher values of these indicators at plot H compared to plot K may be connected to a more varied tree species structure at plot H, with the occurrence of mycotrophic trees other than just beech and fir that are present at plot K (see Table 1).

In Tables 7, 8, we give the number of macromycetes species at plots H and K, where we evaluated the biomass of fruiting bodies in fresh weight during the research period. At plot H, we

evaluated the biomass of fruiting bodies for 58 species (i.e. 66.6% of all species at plot H) where the largest amount of fruiting body biomass was produced by wood-inhabiting fungi (395.71 kg.ha⁻¹). At plot K, biomass was evaluated for 43 species (61.4%) where the largest amount of fruiting body biomass was produced by ectomycorrhizal fungi (386.55 kg.ha⁻¹). It is not surprising that the highest value of biomass at plot H was that of wood-inhabiting fungi, given the ample supply of dead wood substrate at plot H. In contrast, it were ectomycorrhizal fungi that dominated in biomass production at plot K, due to higher values of fruiting bodies abundance and higher average weight of larger specimens, (produced by *Craterellus cornucopioides*, *Cortinarius* spp., *Lactarius* spp. and *Russula* spp.).

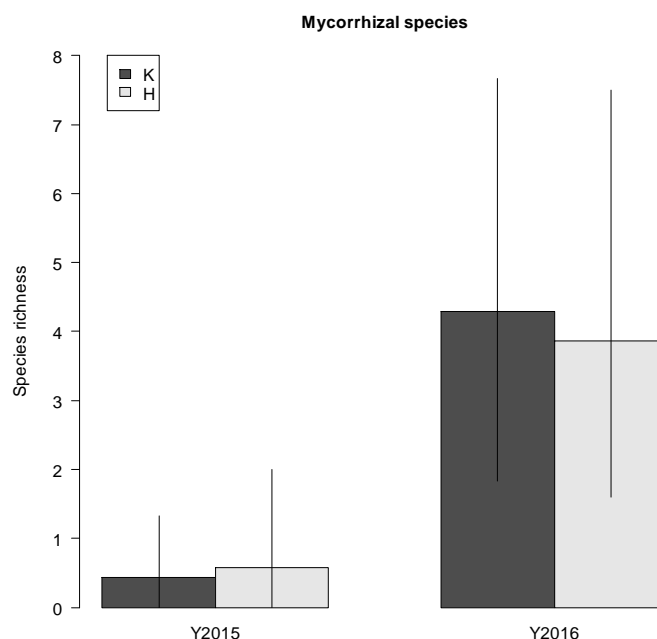


Figure 7 – Mean species richness of mycorrhizal fungi for 100 m² at sites K and H during seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

Table 8 shows that ectomycorrhizal species produced 34.8% of the total biomass at plot H, and 71.3% of the total biomass of fruiting bodies at plot K. To a certain extent, this can be attributed to a higher species diversity of macromycetes and a higher representation of wood-inhabiting fungi at plot H. At the control plot K, lower species diversity and lower proportion of wood-inhabiting fungi was observed, due to the lack of dead wood substrate, with ectomycorrhizal species producing more fruiting bodies of higher average weight.

Table 7 Number of species (Σ), number of species for production evaluation (Prod. Σ , Prod. %) and fruiting body biomass production in the individual ecotrophic groups (kg.ha⁻¹).

Plots	Σ	Prod.	Prod.	WP	WS	TS	EM
		Σ	%				
H	87	58	66.6	3.29	395.71	27.01	227.52
K	70	43	61.4	1.58	142.34	11.53	386.55
Total	117	75	64.1	4.87	538.05	38.54	614.07

WP – wood-inhabiting parasites, WS – wood-inhabiting saprotrophs, TS – terrestrial saprotrophs, EM – ectomycorrhizal symbionts

Table 8 Biomass production of ectomycorrhizal species (EM) and its relation to total biomass production at individual plots (kg.ha⁻¹).

Plots	H			K		
	Total production	EM production	EM (%)	Total production	EM production	EM (%)
Total	653.53	227.52	34.8	542.0	386.55	71.3

Other fungi (terrestrial saprotrophs) and production of selected species

The abundance of other fungi (terrestrial saprotrophs) species was significantly affected by season and there was a significant interaction between site and season (Table 9). The abundance was higher in the season of 2016, but site factor affected the abundance in the season of 2015 (Fig. 8). Similarly, the richness of other species was affected by season, but only marginally, with significant interaction between site and season (Table 9). Species richness was higher in the season of 2016 but higher abundance was observed also at plot H in the season of 2015 compared to the abundance at plot K (Fig. 9). Shannon diversity index in the season of 2016 was not different between the two sites (Table 9). Production of selected fungi species was significantly higher in the season of 2016 (Fig. 10) but there was no significant effect of site on the biomass production (Table 9). Of 117 identified species of macromycetes (Table 2), 27 were included in the group of terrestrial saprotrophs, where the species *Mycena alcalina* agg. produced the most fruiting bodies (52 fruiting bodies), followed by *Mycena inclinata* (50) and *Psathyrella laevis* (38).

Table 9 Results of two-way ANOVA like negative binomial (NB), poisson (GLMp) and linear models (LM) of other (terrestrial saprotrophs) fungi abundance, species richness, Shannon index of diversity and biomass production of selected species of sites K and H in seasons 2015 and 2016 from the EES Kováčová stand. Shannon index was analysed only in season of 2016 as the result of too many zero samples in season of 2015. P values are based on the specific resampling method (see methods).

Type of model/Source	Test statistic	P
NB Abundance	Deviance	
Site	1.31	0.27
Season	6.48	0.01
Site x Season	5.37	0.04
GLMp Species richness	Deviance	
Site	1.30	0.24
Season	3.65	0.06
Site x Season	4.95	0.03
LM Shannon index	F	
Site	0.26	0.62
LM Production	F	
Site	0.04	0.86
Season	8.91	0.004
Site x Season	0.35	0.55

Discussion

Mycological research in the EES Kováčová was regularly carried out also in the past. Comprehensive mycofloristic results from this territory are reported by Mihál et al. (2009) who determined a total of 353 macromycetes species here during the years 1990 to 2008. Mihál (2012a) found that a major part of the group of the most dominant species consisted of wood-inhabiting macromycetes at the EES Kováčová. Thanks to abundant wood substrate left over after harvesting intervention, the portion of wood-inhabiting macromycetes was higher. Relatively low presence of ectomycorrhizal symbionts (22.7%) may follow after negative impacts of harvesting interventions,

removing trees that were mycorrhizal partners of symbiotic fungi and considerable opening of forest stand canopy resulting in soil desiccation at individual research plots. A similar relationship between wood-inhabiting fungi and mycorrhizal symbionts was also found during our research at H and K plots.

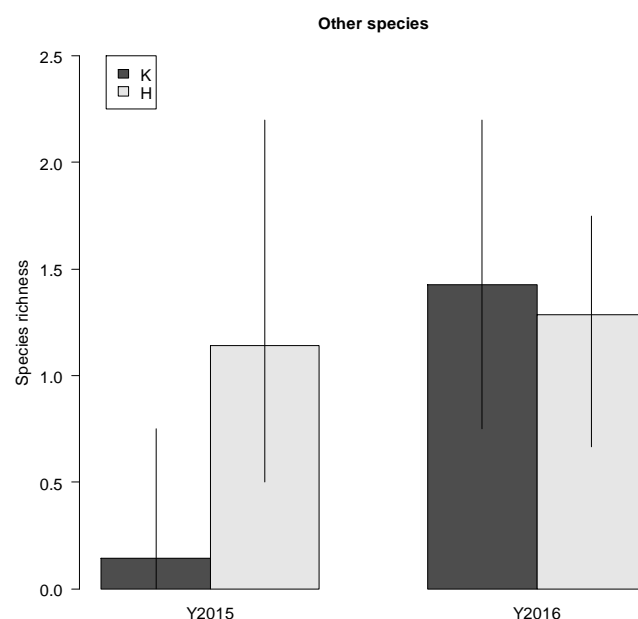


Figure 9 – Mean species richness of other fungi (terrestrial saprotrophs) for 100 m² at sites K and H during the seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

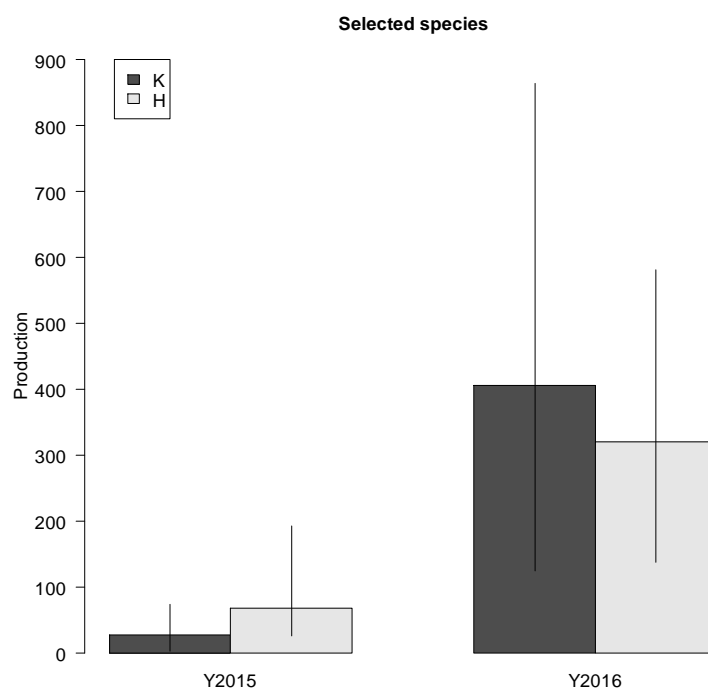


Figure 10 – Mean biomass production of selected species (kg.ha⁻¹) at sites K and H during seasons 2015 and 2016 from the EES Kováčová stand. Error lines denote 95% non-parametric bootstrap confidence intervals for the means.

Baldrian et al. (2016) indicate that the amount of deadwood implicates very diverse substrate in terms of quality and quantity of fungal biomass as well as the species diversity of fungal communities. These authors have noted the presence of several wood-inhabiting species on beech wood; we have also found such occurrence in the EES Kováčová, for example: *Bjerkandera adusta*, *Kretzschmaria deusta*, *Lycoperdon pyriforme*, *Mycetinis alliaceus*, *Pluteus cervinus*, *Resinicium bicolor*, *Trametes versicolor* and others. Abrego & Salceda (2014) note that apart from the tree density, the distance to the nearest edge was also related to forest patch microclimate. We observed a similar process at the edges of plot H, where the positive influence of the density of the beech stand on the species composition of wood-inhabiting fungi was manifested. Abrego et al. (2017) found that the most frequented species are e.g. *Bjerkandera adusta*, *Chondrostereum purpureum*, *Hypholoma fasciculare*, *Mycena* spp., *Mycetinis alliaceus*, *Panellus stipticus*, *Pluteus cervinus*, *Psathyrella piluliformis*, *Stereum hirsutum* etc. These are wood-inhabiting species that also appeared in our collections in managed beech stands (especially at plot H at the EES Kováčová).

Mihál (1994) found that in a submontane beech forest during the three years after harvesting intervention, the portion of wood-inhabiting saprotrophs was the highest (60.0%) at the research plot with clear-fell in the past and the lowest (39.2%) at the control plot with no intervention. There was a large amount of deadwood substrate left at the site after clear-fell that was quickly colonized by wood-inhabiting fungi, whereas these were missing at the control plot with no harvesting intervention with small amount of deadwood substrate. For example, Mihál (1995) noticed that values of fruiting bodies abundance of wood-inhabiting saprotrophs in the thinning stands of beech monocultures was between 52.1% at the control plot with no intervention, compared to up to 83.3% at the plot with free level thinning applied. Mihál & Bučinová (2005) conclude that the groups of the most dominant fungal species consist of almost the same taxa at each plot in EES stands during 2003–2004 (*Ascodichaena rugosa*, *Diatrype disciformis*, *Hypoxylon fragiforme*, *Valsa ambiens*, *Pseudovalsa spinifera*, *Polyporus varius*, *Stereum hirsutum*). These species occurred most frequently and reached high values of both abundance and distribution of fruiting bodies in our research during 2015–2016 as well.

We found an interesting parasitic species, *Biscogniauxia nummularia*, at the EES Kováčová which is an indicator of beech forest stands. Luchi et al. (2015) examined the potential role of *Biscogniauxia nummularia* as a latent factor of *Fagus sylvatica* infestation in Italy. It should be noted that *B. nummularia* was found on dying beech branches at the EES Kováčová (K – control plot). Among other dominant wood-inhabiting fungi in beech forests, Persiani et al. (2016) mention ascomycotic species, which we also found at the EES Kováčová (e.g. *Bisporella citrina*, *Diatrype disciformis*, *Hypoxylon fragiforme*, *Xylaria hypoxylon*). The species *Biscogniauxia nummularia* was also found by Siller et al. (2013) in the primeval forests of the Örség National Park in Hungary and the taxonomically related species *Biscogniauxia succenturiata* was reported by Vasilyeva & Stephenson (2015) from *Quercus mongolica* in south-eastern Russia.

Kutszegi et al. (2015) report fungal species that were strongly associated with beech stands: *Antrodia fragrans*, *Biscogniauxia nummularia*, *Hypoxylon fragiforme*, *Mycetinis alliaceus*, *Polyporus varius*, *Postia subcaesia*, *Skeletocutis nivea*, *Trametes versicolor*, *Xylaria carpophila* and *X. hypoxylon*. Species *B. nummularia*, *T. versicolor*, and *X. hypoxylon* were also correlated with more neutral litter pH and trees with larger mean diameter of the trunk. *Lactarius blennius*, *Pseudocraterellus undulatus*, *Russula emetica* and *Tricholoma ustale* were among the dominant species of beech forest. Most of these species were dominant also in our observation at the EES Kováčová, especially species from the genera *Lactarius* spp. and *Russula* spp. at the K plot. Dvořák et al. (2017) studied macro-fungal diversity patterns in central European forests and their importance in old-growth forests. The authors report that in both managed and unmanaged beech stands, the dominant species were of the genera e.g. *Hypoxylon* spp., *Hypholoma* spp., *Lactarius* spp., *Mycena* spp., *Psathyrella* spp., *Russula* spp., *Stereum* spp. etc. These are representatives of genera that we also recorded as dominant genera at the EES Kováčová.

According to Tyler (1991), beech throughfall has a significant influence on the production of fruiting bodies of terrestrial saprotrophs. For example, in a sufficiently thick layer of beech debris, there was a high production of fruiting bodies by species of the genus *Mycena* and also *Rhodocollybia butyracea* f. *asema*. In the monoculture stand of submontane beech, Mihál & Bučinová (2007) found that the highest fruiting body biomass in terrestrial saprotrophic species were in *Marasmius rotula* (11.21 kg.ha⁻¹) and *Rhodocollybia butyracea* f. *asema* (5.39 kg.ha⁻¹ in fresh fruiting bodies weight) mainly owing to rich debris layer in the stands. Similarly, Salerni & Perini (2004) observed higher production of fruiting bodies of the species *Boletus edulis* in the forest with sufficient layer of debris. Mihál (2012b) assessed the biomass production of sporocarps of macromycetes in a beech stand at the EES Kováčová during 2007 and 2008. He found that the dynamics of biomass production increased from the clear cut (0.86 and 2.23 kg.ha⁻¹) to the densest stands with sufficient layers of debris (44.5 and 248.5 kg.ha⁻¹ fresh mass of fruiting bodies). The biomass production of sporocarps was mostly due to ectomycorrhizal macromycetes, which produced a total of 327.7 kg.ha⁻¹, particularly *Craterellus cornucopioides*, *Lactarius piperatus* and species of the genus *Russula*. Among wood-inhabiting macromycetes, the highest biomass was produced by *Armillaria ostoyae*, *Hypholoma sublateritium* and *Kuehneromyces mutabilis*. Janík & Mihál (2007) studied the ratio between the dynamics of sporocarp biomass production (kg.ha⁻¹) at the EES Kováčová and the dynamics of above-ground biomass production of herbs (t.ha⁻¹) in correlation with the stocking at the partial research plots. They have found that the dynamics of sporocarp biomass increased from the clear cut plot: (5.73 kg.ha⁻¹) to the plot with a stocking of 0.9: (37.39 kg.ha⁻¹ fresh biomass of sporocarps); the trend in herbal biomass was exactly the opposite: (1.2 t.ha⁻¹ at the clear plot, to 0.2 t.ha⁻¹ at the plot with a stocking of 0.9).

In summary, we can conclude that the amount of throughfall is a stronger governing factor for the production abilities of fungal communities than soil temperature. Egli et al. (2010) support the hypothesis that ectomycorrhizal fruiting body production must be linked with the growth of associated host trees. For example, the abundance of ectomycorrhizal fungi of a beech forest increased from 19% to 70% in the thinning stand, while the abundance increased from 38% to 52% in the non-thinning stand. Our results from the EES Kováčová confirm that in the thinning beech stand - plot H, the recorded values of fruiting body abundance (2,803 ex.) were higher than in the oldest control stand – plot K (1,648 ex.). On the other hand, the abundance of fruiting bodies of ectomycorrhizal fungi at the thinning plot H was 4.03 % of the total abundance at plot H, while the abundance of ectomycorrhizal fungi at the control plot K, was 12.0 % of the total abundance at plot K.

Our results show that in the 28-year-old beech pole-sapling stand at plot H, the value of fruiting body relative abundance of all determined species of fungi was higher. At the same time, we recorded higher values of species richness and abundance of wood-inhabiting fungi fruiting bodies at plot H compared to the control plot K mainly due to sufficient amount of dead woody substrate at plot H which we assumed in our working hypothesis. Also, there were higher values of terrestrial saprotrophs recorded at plot H. The majority of indicator species consisted of wood-inhabiting fungi occurring mainly at plot H.

Paradoxically, higher values of mycorrhizal potential and mycorrhizal percentage at plot H did not reflect, for example, on the total abundance of ectomycorrhizal fungi at plot H, but the values were higher for ectomycorrhizal species in the 115-year-old mature stand at the control plot K. Our working hypothesis, predicting higher occurrence of ectomycorrhizal species of macromycetes at plot H (rich woody composition of mycotrophic woods) compared to the control plot K (occurrence of only two types of trees – beech and fir), has not been confirmed by this study. At plot K, values of total fruiting body biomass production recorded for all species (where production was assessed) as well as for biomass of ectomycorrhizal species were higher than values at plot H. This was probably connected with greater occurrence of ectomycorrhizal fungi from genera *Cortinarius*, *Craterellus*, *Lactarius*, *Russula* and others that produce meatier and heavier fruiting bodies, which consequently affects the average weight of a single fruiting body of these genera.

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