

Macrofungi on fallen oak trunks in the Białowieża Virgin Forest – ecological role of trunk parameters and surrounding vegetation

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All groups of macrofungi were recorded on 32 large fallen trunks of pedunculate oak (*Quercus robur*) in various decay stages in the strictly protected zone of Białowieża National Park, Poland. The total number of species was 187 with 4–38 species per trunk. The mycobiota of individual trunks was unique, consisting of a variable set of several frequent species, a high number of infrequent to rare ones, and a considerable proportion of mycorrhizal fungi and species preferring conifer wood. Relations between trunk parameters, surrounding vegetation and fungal occurrences were analysed using multivariate statistical methods. The number of fungal species per trunk was significantly correlated with trunk orientation, which reflects the heat load via forest canopy gap, trunk size parameters, percentage of bark cover and contact with the soil. The species-richest trunks were those covered by bark, of larger volume (thick, long), not exposed to heat from afternoon sun, but, simultaneously, with lower canopy cover. Orientation (azimuth) of the fallen trunks proved to be significant also for the fungal species composition of a particular trunk, which also reflected trunk size characteristics, its moss/bark cover and contact with the soil. Presence of some dominants (*Ganoderma applanatum*, *Mycena inclinata*, *Kretzschmaria deusta*, *Xylobolus frustulatus*) had a significant effect on fungal community composition. Some herbs requiring nutrient-rich soils occurred in the vicinity of trunks with a larger contact area with the soil and in later stages of decay. The process of oak trunk decay in relation to fungi and surrounding vegetation is outlined.

Key words: lignicolous fungi, *Quercus robur*, Europe, fungal diversity, ecology, wood decay, trunk orientation, forest canopy gaps, heat load.

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Holec J., Bělák J., Dvořák D., Kříž M., Kuchaříková M., Krzyściak-Kosińska R., Kučera T. (2019): Makromycety na padlých kmenech dubu v Bělověžském pralese – ekologický význam vlastností kmenů a okolní vegetace. – Czech Mycol. 71(1): 65–89.

Na 32 velkých padlých kmenech dubu letního (*Quercus robur*) v různých stadiích tlení, ležících v přísně chráněné zóně Bělověžského národního parku, byly zaznamenány všechny skupiny makromycetů. Celkem bylo nalezeno 187 druhů, na jednotlivých kmenech 4–38 druhů. Mykobiota každého kmenu byla unikátní a sestávala z několika hojných druhů, velkého počtu nehojných až vzácných druhů a nezanedbatelného podílu mykorhizních hub a druhů jinak preferujících dřevo jehličnanů. Vztahy mezi vlastnostmi kmenů, okolní vegetací a výskytem hub byly analyzovány pomocí mnoho-rozměrných statistických metod. Počet druhů na kmenu byl pozitivně korelovan s velikostními parametry kmenu, stupněm jeho pokrytí borkou a negativně s kontaktem s půdou a jeho jihozápadní orientací, která zároveň určovala oslunění skrz mezeru v porostu. Druhově nejbohatší byly kmene s velkým zakorněním, velkým objemem (tlusté, dlouhé), nevystavené odpolednímu slunečnímu záření, ale zároveň pod nižším zápojem porostu. Orientace kmenů byla významná i pro druhové složení hub, které bylo ovlivněno velikostí kmenu, stupněm jeho pokrytí borkou a mechem a procenty kontaktu kmene s půdou. Přítomnost některých dominantních hub (*Ganoderma applanatum*, *Mycena inclinata*, *Kretzschmaria deusta*, *Xylobolus frustulatus*) měla průkazný efekt na složení společenstva hub na daném kmenu. V okolí kmenů, které měly velký kontakt s půdou a byly v pokročilejších stadiích tlení, se vyskytovaly častěji byliny vyžadující bohatší půdy. Byl popsán obecný proces rozkladu padlých kmenů dubů za součinnosti hub a okolní vegetace.

INTRODUCTION

Oak (*Quercus*) is a widely distributed genus of trees occurring in many forest associations around the world. Both living and dead oaks represent an important source of nutrients and energy for numerous consumers, symbionts and decomposers, above all animals and fungi. Fungal decomposers play a very important role in forest ecosystems (Boddy 2001, Stokland et al. 2012). The process of wood decomposition is controlled by complex mechanisms like priority effects, assembly histories, facilitation, and competition between various fungal species (Ottošson et al. 2014, Hoppe et al. 2016, van der Wal et al. 2016, Hiscox et al. 2018).

In temperate regions of Europe, pedunculate oak (*Quercus robur* L.) is dominant especially in lowlands and hilly areas (Ellenberg 2009). Wood-inhabiting fungi of oak-dominated forests are treated in numerous descriptive works published in the 20th century, summarised by e.g. Kreisel et al. (1985). Runge (1980) formally classified fungal communities on wood of Central European trees including oak. Boddy & Rayner (1983, 1984) and Butin & Kowalski (1983) studied fungi inhabiting oak twigs and Sieber et al. (1995) fungi on stem and twig lesions of *Quercus robur*. Fungi typical of natural oak woods in Germany were listed by Blaschke et al. (2009). Succession of selected macromycetes on decaying trunks

was studied by Runge (1975) and Lindhe et al. (2004). Diversity of macrofungi in Irish oak forests was recently described and evaluated with multivariate methods by O’Hanlon (2011) and O’Hanlon & Harrington (2012). Parfitt et al. (2010) showed that wood-decay fungi are latently present in functional xylem of branches and trunks of a wide range of trees including *Quercus robur*. The process of oak wood decay and the role of fungi was recently elaborated by van der Wal et al. (2015) using 454 pyrosequencing and enzyme assays.

Concerning autecology, the spatial distribution of more conspicuous species on oak trees was described by Sunhede & Vasiliauskas (1996). Oak polypores were elaborated by Vasiliauskas et al. (2003). Several studies describe thoroughly ecological requirements of some oak fungi, e.g. *Phellinus robustus* (Sunhede & Vasiliauskas 2002), *Inocutis dryophila* (Sunhede & Vasiliauskas 2003), *Piptoporus quercinus* (Boddy et al. 2004), *Stereum hirsutum*, *Chondrostereum purpureum*, *Stereum rugosum* and *Xylobolus frustulatus* (Mirić & Stefanović 2018).

Case studies focusing directly on diversity and ecology of fungi on wood of *Quercus robur* are infrequent (Nordén et al. 2004, Iršénaitė & Kutorga 2006, 2007). Data published from South Europe (Bernicchia et al. 2008: Italy) and the USA (Schmit et al. 1999: Indiana; Rubino & McCarthy 2003: Ohio) are less relevant as they originate from other *Quercus* species and different environmental conditions. In this situation, we decided to focus on macrofungi inhabiting thick fallen trunks of *Quercus robur* in Białowieża National Park in Poland. The locality represents one of the largest and best-preserved lowland forests in Europe, where huge oaks up to 400 years old are still present (Faliński 1986). Our focus on larger trunks was based on the fact that large old trees play unique and diverse ecological roles (Lindenmayer et al. 2012) and their mycobiota has proved to be richer in comparison with smaller ones (Lindhe et al. 2004, Iršénaitė & Kutorga 2007). Simultaneously, the Białowieża Virgin Forest is a fungal diversity hotspot with unusually rich mycobiota containing numerous rare fungi and species preferring old-growth forests (for recent summaries, see Karasiński et al. 2009, 2010, Karasiński & Wołkowycki 2015, Karasiński 2016). For all these reasons, it is an ideal place for a case study on the ecology of fungi on decaying oak wood. Our aim was to reveal trunk and habitat factors influencing diversity and ecology of macrofungi on decaying oak trunks.

MATERIAL AND METHODS

Abbreviations. AIC: Akaike Information Criterion values; BNP: Białowieża National Park; BW1–BW32: codes of studied oak trunks; CCA: canonical correspondence analysis; CoCA: co-correspondence analysis; CWD: coarse woody debris; DCA: detrended correspondence analysis; DBH: diameter at breast height;

DD: Daniel Dvořák; E: east; E₂: canopy of shrubs and young trees up to a height of 5 m; E₃: canopy of mature trees; E₃₂: total E₂ and E₃ canopy; FA: folded aspect of fallen trunk azimuth; Fspec: number of fungal species on particular trunk studied; GAM: generalised additive model; GLM: generalised linear model; GPS: global positioning system; HL: heat load (folded SW aspect of open gap); JB: Jan Běťák; JH: Jan Holec; MCPT: Monte Carlo permutation test; MK: Martin Kříž; MKu: Miriam Kuchaříková; N: north; OTU: operational taxonomic unit; PCA: principle component analysis; S: south; TK: Tomáš Kučera; W: west; I, II, III, IV (Latin numerals): particular decay stages of studied trunks.

Study area. Northeastern Poland, Podlaskie Voivodeship, east of the town of Hajnówka, Białowieża National Park (Białowiecki Park Narodowy), strictly protected zone of the BNP (Fig. 1). Basic environmental data (Faliński 1986): elevation 147–172 m a.s.l., soils acidic to neutral, developed on Quaternary glacial deposits with network of rivers and streams, ground water at a depth of 1–4 m, continental climate, mean annual air temperature 6.8 °C (January: –4.7 °C, July: +17.8 °C, absolute amplitude: –38.7 °C to +34.5 °C), mean annual precipitation 641 mm (extremes 426–940 mm). In the period 1986–2007 the mean annual air temperature rose to 7.1 °C (January –3.0 °C, July +19.3 °C, absolute amplitude: –34.6 °C to +34.6 °C), mean annual precipitation 606 mm (Malzahn et al. 2009). Data published by the Institute of Meteorology and Water Management show further changes in mean annual air temperatures and precipitation. In the years 2008–2016 the mean air temperature was 7.7 °C (January –4.0 °C, July +19.1 °C, absolute amplitude: –36.2 °C to +34.8 °C) and the mean annual precipitation was 708 mm. Even though the last decade seems to show a higher precipitation than the previous ones, the year 2015 was exceptionally dry with a total precipitation of only 511 mm. The precipitation in 2016 was much higher mainly due to the high precipitation in winter and early spring as well as a very wet beginning of July. Unfortunately, the time prior to our research was much drier than average, September in particular (Electronic supplement O).

Vegetation of the BNP (Faliński 1986) is represented by a lowland hemiboreal virgin forest highly diverse in flora. Tree dominants are *Carpinus betulus*, *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior* and *Picea abies* (*Fagus sylvatica* is completely absent), mixed with less frequent species like *Acer platanoides*, *Ulmus* spp., *Pinus sylvestris*, *Alnus glutinosa*, *Populus tremula*, *Salix* spp. and *Betula* spp. Some tree individuals reach a remarkable size and age. The vegetation mosaic is formed by mesophilous to thermophilous deciduous forests, mesotrophic, oligotrophic and bog coniferous forests, and deciduous bog and floodplain forests and bush. The current deciduous vegetation is considerably homogenised. Kwiatkowska et al. (1997) documented the expansion of *Carpinus betulus* as the main cause of the decline of heliophilous species. The vegetation

surrounding all studied trunks is represented by the *Tilio-Carpinetum* association. Due to different nutrient and soil moisture conditions, the herb layer varies between its subassociations *typicum*, *stachyetosum*, and *caricetosum* (Kwiatkowski & Gajko 2009).

Studied oak trunks. The field work was carried out in September 12–16, 2016. The trunks were searched for in the oldest BNP forest stands with a high percentage of oak. We selected 32 fallen trunks of *Quercus robur* (Figs. 1, 2) of larger diameters (60–130 cm at breast height). Their decay stage was estimated in accordance with the scale defined by Heilmann-Clausen (2001). Its key characters are given below (shortened):

- 1 – fallen trunks without visible signs of decay, wood hard, bark intact;
- 2 – trunks with minor signs of decay, wood still rather hard, bark starting to break up;
- 3 – trunks with moderate signs of decay, surface wood distinctly softened, bark partly lost;
- 4 – trunks with strong signs of decay but still with \pm original shape, surface wood strongly decayed, bark lost in most places;
- 5 – trunks rotten to almost humified, wood very strongly decayed, either to a very soft crumbly substance or being flaky and fragile.

However, this scale will need a revision in the case of pedunculate oak. Advanced core rot, usually present at the time of tree death, the highly resistant oak wood and the large amount of bark accumulating along lying trunks often create combinations of microhabitats not common in the decomposition of other tree species. It was difficult to classify some trunks into the abovementioned categories. Moreover, freshly fallen trunks (stage 1) as well as strongly decayed ones (stage 5) were rare. Consequently, trunks in stages 2 and 3 prevail in our set of trunks (Fig. 3) and those in stage 5 are absent (another reason for their absence from our dataset was the fact that strongly decayed trunks were hard to distinguish from similarly decayed trunks of other tree species).

Trunk parameters were collected by MKu and TK (Electronic supplements A, B) as follows: geographic position (coordinates measured by hand-held Garmin GPSmap 60CSx device with accuracy \pm 3–5 m), total length (length), diameter at breast height (DBH), number of parts (parts), stump height if present (stump), decay stage (1–5, see above; indicated by Latin numerals in diagrams), contact with the soil in % (soil), bark cover in % (bark), moss cover in % (moss). As for habitat parameters, we recorded the direction of trunk fall from the base to its top (azimuth), canopy of mature trees (E_3 , %, estimated from a rectangle covering the trunk and an extra 1 m on both sides), canopy of shrubs and young trees up to a height of 5 m (E_2 , %, estimated like for E_3) and total canopy cover ($E_3 + E_2$, %). To assess trunk mass we computed derived parameters, based on DBH and length: DBH circle area (diameter²), surface area and volume.

To assess sun exposure and direct solar radiation of the studied trunks based on $\tan(\text{slope}) \times \cos(\text{azimuth} - 180)$ for different slopes and orientations to open

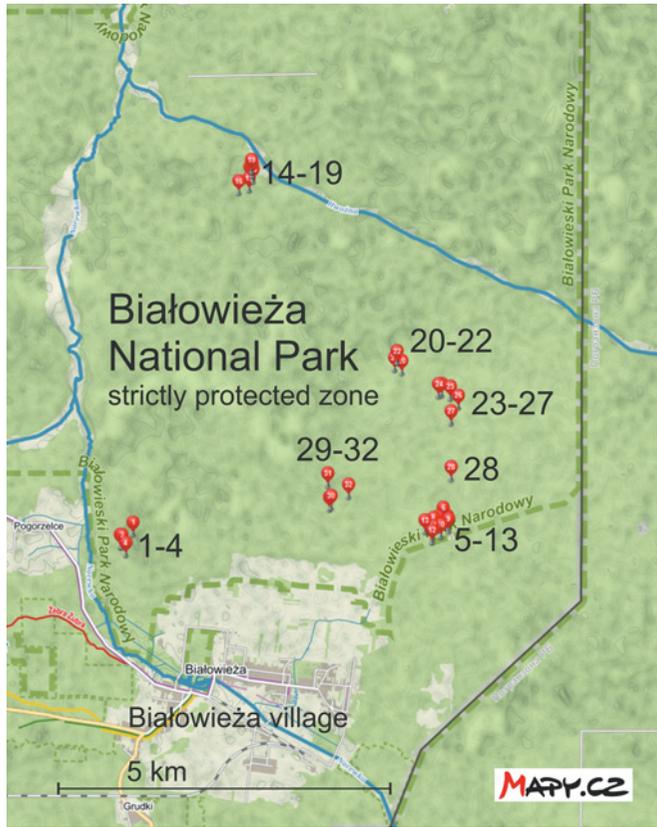


Fig. 1. Study area and position of studied trunks (BW1–BW32) of pedunculate oak (*Quercus robur*) in Białowieża National Park, Poland. For details, see Electronic supplement A. Source of basic map: www.mapy.cz.

gaps in the vegetation canopy (which are created by trunk falls), we recomputed the azimuth of fallen trunk orientation to folded aspect of open gap (McCune 2007). The studied trunks were in horizontal positions, therefore the effect of slope was omitted. The value of folded aspect varied from 0 for northern to 180 for southern direction of the open gap. For direct incident radiation (symmetrical along the N–S axis), the value of gap folded aspect was $FAs = |180 - |azimuth\ of\ fall\ direction - 180||$, where $|$ means absolute value of equation member, and values are in degrees. Afternoon direct radiation is represented by the gap folded aspect for SW orientation (causing the highest ‘heat load’, HL), which is symmetrical along the NE–SW axis ($FAsw [\sim HL] = |180 - |azimuth - 225||$). Additionally, the azimuth of fall direction was similarly folded around the W–E ($F Ae = |180 - |azimuth - 90||$), and NW–SE ($F Ase = |180 - |azimuth - 135||$) axes to include different effects of direct morning radiation.



Fig. 2. Examples of studied trunks of pedunculate oak (*Quercus robur*) in the strictly protected zone of Białowieża National Park, Poland. **a** – trunk in decay stage 1 (BW10); **b** – trunk in decay stage 2 (BW6); **c** – trunk in decay stage 3 (BW17); **d** – trunk in decay stage 4 (BW28); **e** – species-richest trunk (BW5: 38 species); **f** – *Aurantiporus croceus*.

Recording fungi. On each oak trunk studied, we recorded all macromycetes visible with the naked eye, i.e. all occurrences of asco- and basidiomycetes with fruitbodies or stromata larger than ± 2 mm. Such a delimitation of the studied group was chosen among others in order to facilitate comparison with other

studies (see Introduction). Due to the dry September 2016 (see Study area and Electronic supplement O for details), the fructification of fleshy fungi was rather low. Fungi not determinable in the field as well as rare or taxonomically complicated species were photographed in situ, collected, described, dried, studied under a microscope and identified by JB, JH, DD and MK. Vouchers are kept in herbaria PRM (mycological herbarium of the National Museum, Prague, collections of JH, MK), BRNU (Masaryk University, Brno, collections of DD) and the private herbarium of JB (Electronic supplement E). Corticioid fungi collected by JH and MK (except for tomentelloid fungi) were identified by specialist Z. Pouzar (National Museum, Prague). Records of most polypores were revised by polypore specialist P. Vampola (Smrčná). Taxonomy and nomenclature of most species follow Bernicchia & Gorjón (2010), Hansen & Knudsen (2000), Knudsen & Vesterholt (2012), Ryvarden & Gilbertson (1993, 1994), and Ryvarden & Melo (2014). Recent taxonomic monographs on particular genera were consulted.

Vegetation description. The vegetation around selected oak trunks was described with phytosociological relevés. Data were recorded by TK (Electronic supplement F) using the Braun-Blanquet phytosociological method (Kent 2012). Plant cover was estimated separately for tree (E_3), shrub (E_2) and herb (E_1) layers on an area of 225 m² (15 × 15 m) using the nine-degree Braun-Blanquet ordinal scale of cover-abundance values: 1 (rare), 2 (less than 1% cover), 3 (1–3%), 4 (4–5%), 5 (6–15%), 6 (16–25%), 7 (26–50%), 8 (51–75%), 9 (76–100%).

Statistical evaluation. The generalised linear modelling in R (R Core Team 2018) with Poisson distribution and log-link function was used to assess the variables affecting fungal species richness (for details, see Electronic supplement G). As we detected multicollinearity of some explanatory variables, the regression analysis was performed with matrix plots and Pearson pair-wise correlations between explanatory variables. Bark cover of studied trunks was negatively correlated with their decay (−0.45, $p < 0.01$ **) and canopy cover (−0.62, $p < 0.001$ ***), while decay was positively correlated with increasing contact with the soil (+0.41, $p < 0.05$ *), and moss cover (+0.37*). Therefore, the multicollinear decay (expressed on ordinal scale) was complemented by a categorical dummy variable including the different decay stages. Moss cover was related with shrub cover (+0.36*) and trunks under higher canopy cover had a larger contact area with the soil (+0.49**).

Species occurrence matrices of fungi and vegetation were analysed using gradient analyses in the Canoco 5 software (ter Braak & Šmilauer 2012, Šmilauer & Lepš 2014). Collinearity of centered and standardised explanatory trunk and habitat variables was inspected by means of principle component analysis (PCA), which separated groups of response variables along orthogonal axes, similar to groups resulting from the regression analysis (see above). In species analyses,

singletons and doubletons were deleted due to their rare occurrence (on one or two trunks or in their vicinity, respectively). Unconstrained detrended correspondence analysis (DCA) of fungal species composition showed a regular dispersion of trunks (Electronic supplement J), which was independent of spatial position (Fig. 1) and therefore meant a negligible effect of spatial autocorrelation (Electronic supplement K). Neighbour-clustered trunks differed in decay stage and other parameters. The total lengths of largest distance measured by DCA were 3.39 (fungi) and 2.21 (plants), which allowed us to use unimodal ordination methods. A multivariate constrained method, namely canonical correspondence analysis (CCA), was used to analyse the relationship between the fungal species pattern and partitioned variation of trunk and habitat predictors (Legendre & Legendre 2012). The CCA of the influence of dominant fungal species on fungal assemblages used the presence/absence of dominant species as an explanatory variable after extraction of the fungus from the species table. The explanatory effects of particular environmental variables were evaluated with Monte Carlo permutation tests (MCPT, number of permutations was assigned to 999) using the forward selection procedure which selected variables with the best fit of species data. Collinearity was avoided using adjusted p-values. Symmetric co-correspondence analysis (CoCA) was used to compare fungal and plant species patterns.

RESULTS

Fungal diversity

The total number of fungal occurrences on 32 trunks studied was 792. We recorded 187 species of macrofungi (Electronic supplement D). Macroscopic ascomycetes were represented by 7 species and basidiomycetes by 180 species. The species-richest genera were *Mycena* (20 species), *Tomentella* (13), *Botryobasidium* (8), *Hyphodontia* (8), *Pluteus* (6), *Trechispora* (6), and *Entoloma* (5). The most frequent species were *Hymenochaete rubiginosa*, *Phaeohelotium monticola*, *Xylobolus frustulatus*, *Mycena inclinata* and *Mycena galericulata* (found on more than 70% of trunks; *H. rubiginosa* on 88%). On the other hand, 84 species (44%) were found on 1 trunk only, 36 species on 2 trunks, and 19 species on 3 trunks. Species occurring on 1–3 trunks represented 74% of the total fungal diversity. This means that the species composition on each trunk is rather specific, consisting of several frequent species plus a variable set of infrequent ones.

The mycobiota consisted especially of corticioid and agaricoid fungi. These fungi often produced fruitbodies on decaying pieces of wood and bark lying on the soil below the trunks. The more decayed trunks and woody debris from them were also occupied by mycorrhizal fungi, e.g. agarics (*Amanita*, *Cortinarius*,

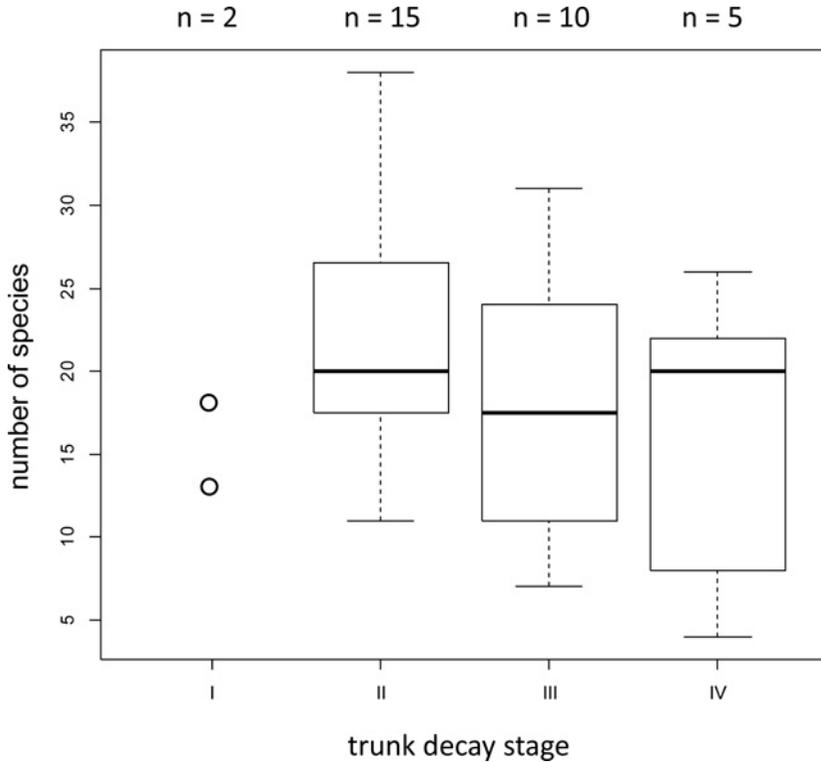


Fig. 3. Range of fungal species richness of all studied trunks in relation to particular stages of trunk decay (I–IV; n: number of studied trunks). No significant difference in fungal richness between decay stages was detected.

Hebeloma, *Inocybe*, *Laccaria*, *Lactarius*, *Paxillus*, *Russula*, *Tricholoma*), plus *Clavulina*, the gasteromycetoid *Scleroderma*, resupinate fungi (*Amphinema*, *Byssocorticium*, *Pseudotomentella*, *Tomentella*), and several ascomycetes (*Helvella*, *Humaria*). In total, 37 species of mycorrhizal fungi (20% of the total number of species) were found. Interestingly, the group of polypores was rather species-poor, including a small group of polypores with large fruitbodies (*Aurantiporus croceus*, *Laetiporus sulphureus*, *Phellinus robustus*, *Piptoporus quercinus*, *Trametes gibbosa*) and several resupinate species of the genera *Antrodia*, *Datronia*, *Perenniporia*, *Physisporinus*, *Rigidoporus*, *Schizopora* and *Trechispora*. Ascomycetes with larger fruitbodies or stromata were infrequent (7 species of the genera *Ascocoryne*, *Cudoniella*, *Helvella*, *Humaria*, *Kretzschmaria*, *Phaeohelotium* and *Xylaria*). However, small ascomycetes not recorded by us (e.g. *Mollisia*, *Orbilina*, etc.) would add further species to the total fungal diversity.

Individual trunks hosted 4 to 38 species of macrofungi (Electronic supplement C). Trunks inhabited by 30–38 species were in decay stages 2 and 3 with the three richest ones in stage 2. However, the fungal richness of trunks in stage 2 varied considerably as they hosted both a low (11) and a high (38) number of species. Trunks with a low number of species (4–9) were in decay stages 3–4.

Trunk parameters and fungal richness

We tested pairwise correlations between all trunk and habitat parameters and fungal richness. The number of fungal species is significantly (negatively) correlated with a SW direction of trunk fall, which represents the highest gap heat load ($r = -0.49$, $p < 0.01$ [**]). Trunk size parameters (correlation with diameter $+0.41$, $p < 0.05$ [*]) are also significant. Of the studied trunks (60–130 cm in diameter), those with a diameter below 97.5 cm host 16.1 species on average whereas thicker trunks host 24.5 species on average.

The possible collinearity of trunk parameters was additionally detected using PCA (Fig. 4). In this diagram, the correlation structure between these variables is seen. The gradient of decay from the right low quadrant to the upper left quadrant represents a temporal succession scale. The most important factor for the higher number of fungal species (Fspec) is a group of trunk parameters represented by percentage of bark cover (which is negatively related to the canopy cover and relative contact area with the soil, all these variables also reflecting decay). Another important group relating to fungal richness consists of trunk diameter, stump height and number of trunk parts (the last two parameters having a significant effect, $p < 0.01$, but are present in 4 trunks only, therefore we do not use them in further considerations). This group is negatively correlated with folded SW aspect for open gap heat load (HL) and tree layer cover.

Generalised linear and additive models estimating the total richness of fungal species show an integrated role of decay stage and trunk size parameters (diameter²: circle area of DBH, Electronic supplement I), with an additional linear effect of length and other trunk mass parameters (volume, surface), folded aspect of gap heat load, moss and shrub covers (compare different complexity degree in individual models, Electronic supplement H). The number of fungal species on particular trunks does not significantly depend on concrete decay stages. A slight trend is seen in Fig. 3, showing the highest number of species on trunks in stage 2 and a subsequent slight decrease in stages 3 and 4 (trunks in stage 4 show higher variance in number of species), but it is biased by the uneven number of trunks studied in particular decay stages (Fig. 3).

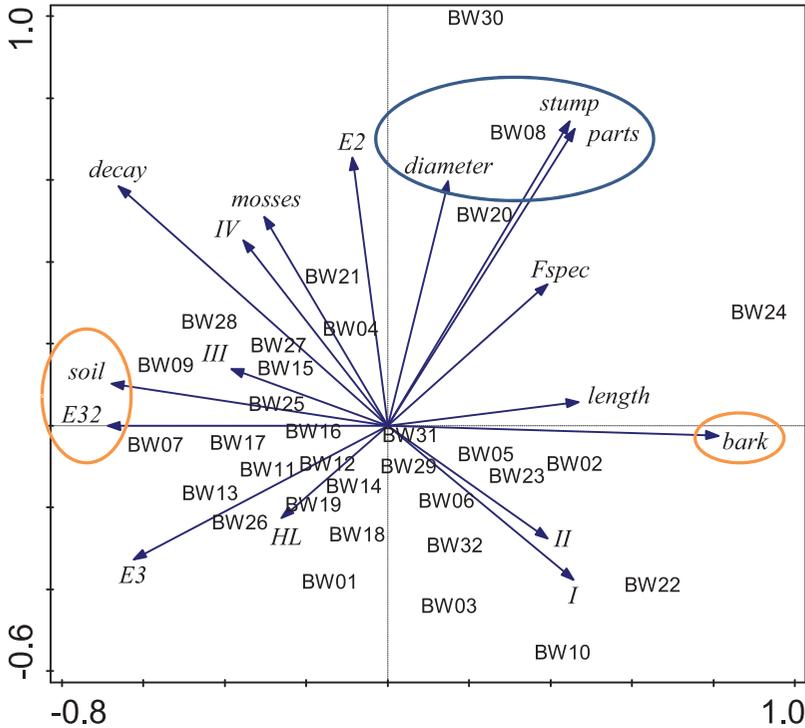


Fig. 4. Unconstrained ordination biplot (PCA) of trunk parameters with positions of individual trunks. The clumped arrows (highlighted by left and upper ellipses) show common effects of the parameters. The angle between arrows indicates pair-wise correlations, which are negative in opposite direction. For abbreviations, see Material and methods.

Pattern of fungal species occurrence

The composition of frequent fungal species (without single- and doubletons) reflects the general results regarding total species richness (see Fig. 4, supplements J, K). The main habitat gradient (Fig. 5) relates to gap heat load (which is negatively correlated with total fungal species richness). The species *Hydropus floccipes*, *Mycena speirea* and *Pluteus podospileus* are associated with a high species richness on trunks. In opposite direction, species-poor trunks are present, which are characterised by a high HL. Heat-exposed trunks are associated with e.g. *Resinicium furfuraceum*, *Mycena inclinata* and *Hypholoma fasciculare*. The second main gradient (Figs. 4, 5, supplement K: along Y axis) is represented by trunk size characteristics (diameter, length, number of parts, presence of a stump), their moss/bark cover and contact with the soil. Species of long, bark-covered trunks (Fig. 5: upper part of the diagram) are e.g. *Kretzschmaria deusta*, *Ganoderma applanatum* and *Tomentella sublilacina*. In the lower part

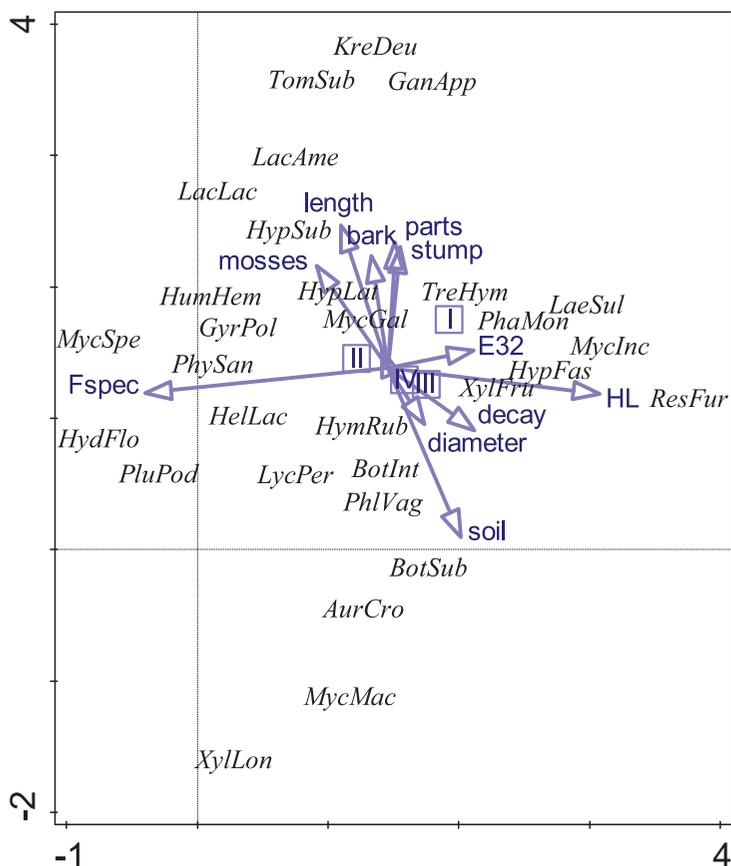
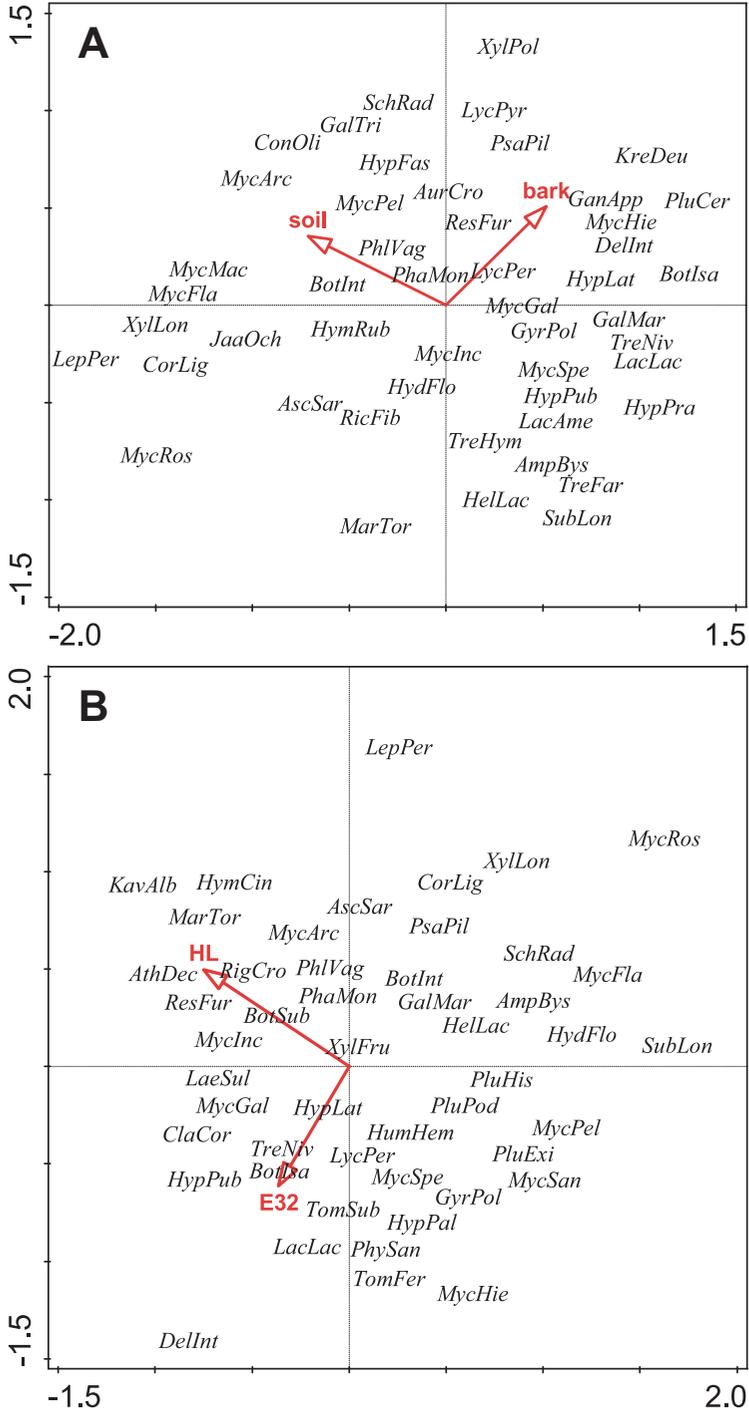


Fig. 5. DCA with frequent fungal species and passively projected trunk and environmental parameters. The total species richness (Fspec: total number of fungi per trunk including single- and doubletons) decreases along the first ordinal axis (X). Parameters not favourable for fungi increase in opposite direction (higher tree and shrub cover and higher gap heat load index). The second axis (Y) covers trunk parameters. Both first and second axes explain 15% of species variation. See also Electronic supplements J, K. Individual decay stages are marked by Latin numerals. For full names of fungi, see Electronic supplement D, for abbreviations of parameters, see Material and methods.

of the diagram, high-diameter trunks having a large contact area with the soil are present, associated with e.g. *Aurantiporus croceus*, *Botryobasidium subcoronatum*, and to a lesser degree with *Phlebiella vaga* and *Botryobasidium intertextum*. Trunk decay stage has a low direct effect on fungal species patterns.

We compared the effects of trunk and habitat groups as predictors in variation partitioning. Constrained analysis CCA (Fig. 6) highlighted more specialised species, having significant relation to both the trunk and habitat characteristics. Bark cover and relative contact area with the soil, together explaining 3.9%



($F = 1.6$, $p < 0.001$, see Fig. 6A), and heat load with total canopy cover, explaining 4.2% ($F = 1.7$, $p < 0.001$, Fig. 6B) of the fungal species pattern, were chosen using the forward selection approach (separately for each group). A negative fraction of intersection of both groups indicates that trunk and habitat predictors, if considered together, explain the fungal species pattern better than the sum of the individual effects of group variables (7.3%, $F = 1.6$, $p < 0.001$). In the upper right quadrant (Fig. 6A), species found on trunks with a high bark cover (connected with lower decay stages) are situated, e.g. *Xylaria polymorpha*, *Pluteus cervinus*, *Galerina marginata* and *Kretzschmaria deusta*. In the opposite upper left quadrant, species of later decay stages typical by their larger contact area with the soil are placed. The group of species connected with a high canopy cover (lower part of Fig. 6B) is rather rich. This group is mainly represented by corticioids and agarics with tiny basidiomata. In the upper left quadrant of Fig. 6B, species of trunks with a high heat load, i.e. more exposed to the sun (but also to precipitation via forest gaps) are found, e.g. *Kavinia alboviridis*, *Hymenochaete cinnamomea*, *Marasmius torquescens* and *Athelia decipiens*. These diagrams (Fig. 6) have a higher explanatory value as for the ecological niche of the depicted fungi (the niche being defined by selected explanatory variables) than the previous one (Fig. 5). Interestingly, some distinctive species like *Aurantiporus croceus*, *Hydropus floccipes* and *Xylobolus frustulatus* are in a central, 'intermediate', position in the diagrams. As shown in the previous paragraph, individual levels of decay stage do not have a direct significant effect on species composition. However, there are some differences (Electronic supplement J). Decay stage 2 situated in the left part of the biplot differs from stages 3 and 4, which overlap (but stage 4 includes more species).

We explored whether the presence/absence of some fungal dominants (i.e. species occurring on a higher number of trunks and forming large or many fruitbodies) influences species composition of a trunk. Of the tested species, *Ganoderma applanatum* (p -ratio = 0.01), *Mycena inclinata* ($p = 0.025$), *Kretzschmaria deusta* ($p = 0.037$) and *Xylobolus frustulatus* ($p = 0.05$) had a significant effect, whereas *Laetiporus sulphureus* and *Aurantiporus croceus* were not significant. However, the presence of species with the strongest effect,

◀ **Fig 6.** Ordination biplots (CCA) with fungal species. Only significant explanatory variables are displayed for trunk (A) and habitat (B) groups of characteristics. For full names of fungi, see Electronic supplement D, for abbreviations of parameters, see Material and methods. The fifty fungal species with the highest fit are projected.

A: Contact with the soil explained 5.3% of total variance [F -ratio = 1.7, P -value = 0.002, P (adjusted) = 0.008], bark cover explained 4.4% (1.4, 0.019, 0.076). The first two axes cover 9.7% of fungal cumulative variance (adjusted 3.5%).

B: Heat load (HL: 5.2%, 1.6, 0.002, 0.012) and total canopy cover (E_{32} : 4.7%, 1.5, 0.01, 0.06); first two axes cover 9.9% (adjusted 3.6%) of fungal variance.

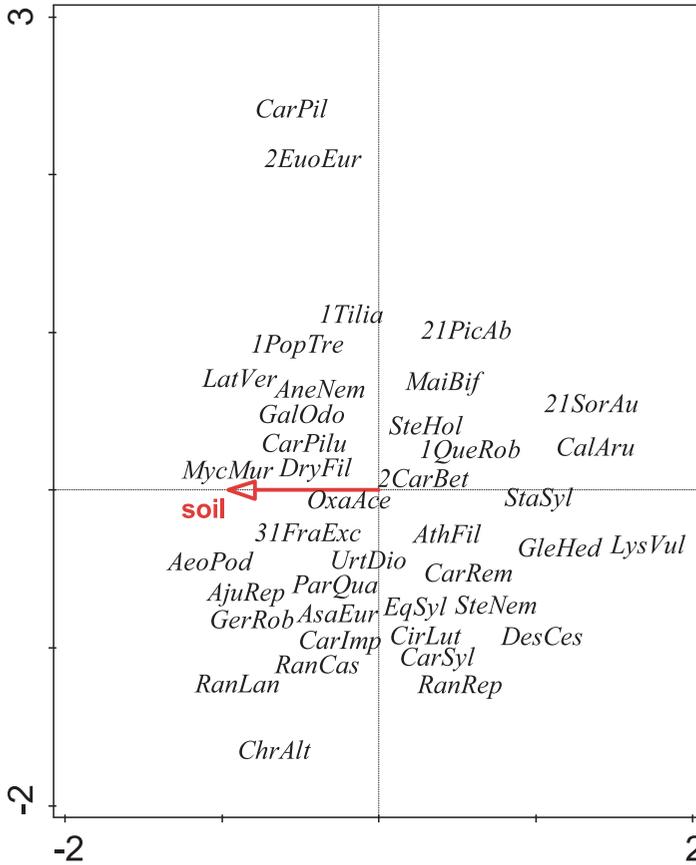


Fig. 7. First two axes of CCA biplot of plant species pattern with the only significant trunk parameter: contact with the soil. This parameter explains 5.1% of species variance on the first constrained axis (X). Thirty species with a higher fit are projected. The species in the left part of the diagram are typical of nutrient-rich mesic soils. For full names of plants, see Electronic supplement F.

Ganoderma applanatum (Electronic supplement L), does not influence the total species richness (including single- and doubletons).

Vegetation characteristics of fungal habitats

Most of our vegetation relevés represent various subassociations of the *Tilio-Carpinetum* association in which shade-tolerant species prevail. The plant species richness corresponds to the E direction of the trunk fall and its volume. Surprisingly, no effect of forest lighting was found in the SW direction. A higher proportion of shrub cover only had a low effect on both plant and fungal species richness (through shadowing). The plant species pattern in unconstrained DCA

generally reflects two main ecological gradients – soil moisture and nutrients (Electronic supplement M). After removing spatial covariance, no trunk parameter affects the plant species pattern except for contact with the soil (F-value = 1.6, p-ratio = 0.023). Plants requiring nutrient-rich soils occur in the vicinity of trunks having a larger contact area with the soil and later decay stages (Fig. 7). The shared CoCA analysis of fungal and plant communities showed non-significant cross-correlations, but supported the relation of some plants to enriched soils (Electronic supplement N).

DISCUSSION

Fungal diversity

The number of 187 species recorded on just 32 oak trunks during one visit represents a rather high fungal diversity. It seems that the results were not substantially negatively influenced by the dry September 2016, as the previous months were rich in precipitation (Electronic supplement O) and lignicolous fungi could have used the water accumulated in the wood before. We suppose that the portion of agarics and corticioids with ephemeral fruitbodies not observed by us due to the September drought was negligible.

Works using permanent plots/sites each containing several dead wood units (e.g. stumps, logs, branches; but mostly of smaller volume than in our case) usually report 70–100 species (Tab. 1) with a peak of 203 species (Iršénaitė & Kutorga 2006, 2007). The reasons for high diversity found out by us were certainly the large size of the studied trunks (documented also in our trunk size gradient, see Results) plus the detailed way of our field work focused on all groups of macrofungi including tiny agarics, corticioids and heterobasidiomycetes, and also on mycorrhizal fungi fructifying on rotten oak wood and wood debris (usually omitted in previous works). Such a detailed approach was used only by Nordén et al. (2004) and partly Grosse-Brauckmann & Grosse-Brauckmann (1983). Another reason seems to be the high fungal richness of the Białowieża Virgin Forest (Karasiński et al. 2009, 2010, Karasiński & Wołkowycki 2015, Karasiński 2016), which represents a huge pool of spreading mycelia and spores of more than 1800 macrofungal species.

Using 454 pyrosequencing of ITS, van der Wal et al. (2015) discovered 447 fungal OTUs (among them 262 ascomycetes and 148 basidiomycetes) in 46 decaying stumps of *Quercus robur* in the Netherlands (young stumps up to 5 years after cutting, i.e. initial stages of wood decay, diameter 20–22 cm). These results are not comparable with ours, as they were obtained by a different method from another kind of substrate, but suggest that real fungal diversity in oak wood is much higher

than diversity documented by fruitbody-based research. However, the dominance of basidiomycetes over ascomycetes in later decay stages observed by us agrees with formerly published data (e.g. Nordén et al. 2004, Iršénaitė & Kutorga 2006).

Tab. 1. Overview of published data on biodiversity of fungi on decaying oak wood (mostly *Quercus robur*) in Europe. The studies are arranged according to the number of visits.

Source	Years of study	Number of visits	Number of trunks / wood units / plots	Number of fungal species	Studied groups of fungi
This study: Poland	1	1	32 trunks (1 site)	187	All macrofungi with fruitbodies larger than 2 mm in diameter
Běĺák 2016: Czech Republic	1	3	32 trunks (1 site)	165	All macrofungi with fruitbodies larger than 2 mm in diameter
Iršénaitė & Kutorga 2006, 2007: Lithuania	2	1 per plot	321 units (46.5 m ²) of coarse woody debris of oak in 50 plots (10 sites)	203	All macrofungi
O'Hanlon & Harrington 2012: Ireland	2–3	4–6	5 plots (5 sites)	94	All macrofungi with fruitbodies larger than 5 mm in diameter
Grosse-Brauckmann & Grosse-Brauckmann 1983: Germany	3	20	1 site, traditional field survey	71	Aphyllophorales, other groups of macrofungi less intensely
Županić et al. 2009: Croatia	3	?	4 sites, traditional field survey	72	Macrofungi with conspicuous fruitbodies

Our dataset contains many oak specialists and oak-favouring fungi, both common species like *Hymenochaete rubiginosa*, *Mycena inclinata*, *Laetiporus sulphureus*, and generally rare ones (Vasiliauskas et al. 2003, Blaschke et al. 2009) like *Aurantiporus croceus*, *Hydropus floccipes*, *Perenniporia medullapanis*, *Piptoporus quercinus* and *Vararia ochroleuca*. It also includes opportunists (*Pluteus cervinus*, *Hypholoma* spp., *Mycena galericulata*, etc.). Surprisingly, quite a lot of species usually preferring spruce or generally coniferous wood were recorded (*Botryobasidium intertextum*, *Crustoderma dryinum*, *Gloeopeniophorella convolvens*, *Hyphodontia abieticola*, *Jaapia ochroleuca*, *Rigidoporus crocatus*, *Scytinostromella heterogenea*). Their occurrence on oak trunks in the Białowieża Forest is presumably enabled by the specific tree composition of hemiboreal forests, where spruce and oak have co-existed for thousands of years since the late Holocene (Milecka et al. 2009), and also by the long period without human intervention, which has led to an extraordinary number of various substrates for lignicolous fungi. Several species not listed for BNP by Karasiński et al. (2010) were also documented during our study. We will focus on them in a separate study in the future.

Trunk parameters and fungal richness

Analysis of our data highlighted that the species-richest trunks are voluminous (thick, long), with a high bark cover, and in younger stages of decay. Such trunks are exposed to direct precipitation due to the gap in forest canopy caused by the fall of the tree (until the gap is closed by the growth of surrounding shrubs and trees). Additionally, high fungal richness is supported by trunk fragmentation (stump + log or trunk broken into two or more parts). Surprisingly, orientation of the fallen trunks also proved to be very important. We found that the species-richest trunks were oriented 'properly', i.e. in north-east directions (N, NE, E) representing a minimal heat load through the gap. Vegetation surrounding such gaps protects especially large lower trunk parts from direct sun radiation (especially the afternoon sun) and consequent desiccation (which has a negative effect on fungal fructification and/or occurrence). Lindhe et al. (2004) also studied the influence of sun exposure on fungal richness. They found that numbers of species were not related to the level of sun exposure. However, their study was carried out under different habitat conditions (cut stumps and logs). The importance of wood moisture and fungal richness on oak wood decay was recently stressed by van der Wal et al. (2015).

The positive effect of oak CWD volume on fungal richness was also mentioned by Iršėnaitė & Kutorga (2007) and Lindhe et al. (2004). In a study from Ohio, USA, Rubino & McCarthy (2003) further showed that fungal species richness was positively correlated with volume of woody debris in the study plot and with volume of studied logs, amount of bark, and amount of fragmented wood. It seems that the trunk parameters shown to be significant for fungal richness in our and other studies are of general validity, at least for oak CWD.

Concerning the heat load, the afternoon direct solar radiation causes higher temperature maxima than equivalent morning radiation. Geiger et al. (2003) mention near-ground temperatures to be up to 5 °C higher in comparison with shadowed stands, depending on the ratio of gap diameter to height of surrounding stand. Indeed, we found that a SW orientation of the studied trunks (and gaps which they create during the fall) has a significantly negative effect on species richness. This is also connected with the fact that a falling tree crown creates a wider gap in its SW part which enlarges the sun exposure of the lower tree half (especially from the most intensive afternoon radiation). Moreover, gap size influences the amount of precipitation. Slavík et al. (1957) documented that rainfall below trees was about 20–30% lower in comparison with the gap centre, while rainfall on the SW gap edge was increased by over 100% by transmission of precipitation by wind. Optimal gaps have a ratio of diameter to height of surrounding stand in the range 1–2 (Geiger et al. 2003, Muscolo et al. 2014). Such gaps exhibit a lower direct sky view and longwave radiation loss, lower evaporation, better

protection against wind and late frosts, higher nocturnal temperature minima and dew point (affecting air humidity). All these microclimatological characteristics differ on shaded southern vs. sunny northern edges of the gap (Geiger et al. 2003). Consequently, the fallen trunks represent a continuous gradient of microclimatically diverse microhabitats (along their length).

Pattern of fungal species occurrence

Our data show that the fungal community composition on particular trunks is significantly influenced by gap orientation and resulting heat load. Trunks exposed to more intensive afternoon sun radiation have a different (and species-poorer) mycobiota than the shaded, more species-rich ones, inhabited by e.g. *Hydropus floccipes*, *Mycena speirea* and *Pluteus podospileus*. As far as we know, the role of fallen trunk orientation on their fungal richness and species pattern has not been paid attention to date.

Further important factors are trunk size parameters, canopy cover, percentage of bark and moss cover and relative contact area with the soil. The influence of these parameters on fungal communities has not been assessed in detail in traditional ‘oak’ studies. Iršénaitė & Kutorga (2006) only stressed the role of wood decay stage. They showed that there is a difference in community composition between early (1–2) and later (4–5) stages (principally the same situation was described by van der Wal et al. 2015), but no strong preference of most fungal species for wood of a particular decay stage. Van der Wal et al. (2015) showed in their molecular study that key factors of decay rate change in time: the variance of decay rate in initial sapwood is significantly correlated with wood moisture content, whereas it is related to the composition and OTU richness of the fungal community in later stages.

Our data also show that wood decay stage has a low direct effect on community composition. We observed that the decay of thick oak trunks considerably differs from e.g. beech or spruce (Renvall 1995, Heilmann-Clausen 2001). It often starts simultaneously from the surface (by decortication and subsequent decay or separation of thin wood layers, forming wood debris below the trunk, which often hosts interesting fungi) and in the inner trunk part (resulting in creation of a large central cavity). Consequently, estimation of the ‘average’ decay stage of the whole trunk (especially of stages 2–4) was not easy. In some cases it was a compromise between wood hardness and overall trunk appearance. This ambiguity is probably also a reason why some common species, generally preferring later stages of wood decay (e.g. *Pluteus cervinus*, *Galerina marginata*) occupied trunks covered with bark (see Fig. 6A). In fact, their mycelium probably favoured more decayed wood inside such trunks.

Boddy (2001) showed that fungal decomposers have a great effect on the wood decay process. Their interactions, above all competition (recently stressed by e.g. van der Wal et al. 2016 and Hiscox et al. 2018), result in highly variable fungal communities, differing in each wood unit (Kubartová et al. 2012, van der Wal et al. 2015). Our analyses show considerable influence of some dominant species (*Ganoderma applanatum*, *Mycena inclinata*, *Kretzschmaria deusta*, *Xylobolus frustulatus*) on fungal community composition. The differences are most probably explainable by the competitive power of these species. Another reason for community variation is the random way of fungal spread (via spores or mycelia) and the presence of some wood-decaying species already in living trees (Parfitt et al. 2010).

Trunks, their decay, and surrounding vegetation

All of the studied trunks were situated in a generally closed forest stand. However, the canopy cover directly above individual trunks differs considerably (Electronic supplement B). Initially, the fall of either a living or a dead trunk (by uprooting or breakage) opens the tree and shrub layer by creating a canopy gap. If the fallen trunk still has thick branches, it is mostly not in full contact with the soil, as the branches lift it from the soil surface. Later on, the trunk slowly 'sits' down on the floor (the supporting branches slowly disappearing by breakage or decay), decorticates (also due to the fungal activity), and is covered by mosses (simultaneously its fungal richness slowly decreases).

The different shading described in previous chapters has an effect on plant species richness. Our data showed that plant richness increases with eastern orientation of the gap (morning radiation, Electronic supplement H). The trunk volume also has an important effect on plants (similar to the case of fungal richness). Larger trunks create larger gaps and enhance the abovementioned effects. During this initial phase, shading caused by a higher proportion of shrubs has a positive effect on plant richness. Later on, the surrounding shrubs and trees continue to grow and finally close the canopy gap. The revegetation process is accelerated not only by eastern orientation of the fallen trunk, but probably also by an increasing amount of available water and nutrients which are not extracted by living large trees. The increasing cover of the shrub layer positively affects fungal richness only in the initial decay stages (shading and consequent lower gap heat load). Longer lying trunks are gradually overgrown by shrubs and trees, thus sheltered from rainfall, and both plant and fungal richness decrease (Fig. 3, Electronic supplements H, K).

Trunks in advanced decay stages have a larger contact area with the soil (Fig. 4), which can potentially enrich the soil below and around the trunk. Our results show that nutrient enrichment is reflected by the surrounding plants, where

species requiring a higher level of nutrients and moisture prevail (Fig. 7). This agrees with data by Chečko et al. (2015), who reported an increase in local plant species cover and frequency directly on logs and their surroundings, with some species facilitating deadwood decomposition. Similarly, the plant species reported as the most frequent by them were similar to the species occurring in our vegetation samples around trunks with a larger contact area with the soil. However, Harmon & Hua (1991) documented slower decomposition and a temporal lag of nutrient release from woody debris in comparison to litter.

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