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Report from a mycodiversity hotspot – macrofungi on decaying trunks of Norway spruce in the Białowieża virgin forest, Poland

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All groups of macrofungi were monitored on 32 decaying trunks of Norway spruce in Białowieża National Park, Poland. Spruce is a declining keystone species there. By means of a fruitbody-based survey, we captured 272 species in total, with 11–63 species per trunk. We registered 59 species of the Polish Red list and 30 species unpublished from Białowieża National Park, especially ones with inconspicuous fruitbodies. Detailed monitoring proved to be an effective way to capture them. The species number on individual trunks was significantly correlated with decay stage, shrub cover above the fallen trunks and trunk diameter. The most species-rich trunks were those in decay stages II and III, simultaneously having the largest diameter and shrub cover. These had the highest diversity, some even in comparison with previously published data. The species composition significantly reflected the different decay stages, trunk contact with the soil, trunk diameter, and shrub cover. Increased shrub cover was accompanied by a rich occurrence of corticioids and small agarics, apparently supported by a humid microclimate under the canopy of young trees. A total of 48 species were classified as generally rare, preferring natural forests, or associated with boreal/montane ecosystems. The most interesting of them, e.g. *Amylocystis lapponica*, *Antrodiella citrinella*, *Crustoderma dryinum*, *Fomitopsis rosea*, and *Steccherinum gracile*, were mainly associated with trunks having less contact with the soil. The funga of dead spruce wood in the Białowieża forest is enormously rich. It is distinguished by the occurrence of some extremely rare species (*Cyphelloporia bialoviesensis*, *Gloeocystidiellum sibiricum*, *Mucronella pulchra*) and rare boreal or boreal-montane elements (*Asterodon ferruginosus*, *Boreostereum radiatum*, *Ceriporiopsis jelicii*, *Dichostereum boreale*, *Pycnoporellus alboluteus*, *Tricholomopsis sulphureoides*). To preserve this diversity, measures will be needed at both the global and local level.

Key words: *Picea abies*, *Basidiomycota*, *Ascomycota*, diversity, ecology, old-growth forests, hemiboreal forest, Europe.

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Všechny skupiny makromycetů byly monitorovány na 32 tlejících kmenech smrku ztepilého v Bělověžském národním parku v Polsku. Smrk je zde klíčovým, ale ubývajícím druhem. Na základě výskytu plodnic jsme podchytili 272 druhů hub při 11–63 druzích na kmen. Zaregistrovali jsme 59 druhů z polského červeného seznamu a 30 druhů dosud nepublikovaných z Bělověžského národního parku, zejména ty s nenápadnými plodnicemi. Detailní monitoring se ukázal jako účinný způsob, jak je zachytit. Počet druhů na jednotlivých kmenech byl významně korelován se stadiem tlení, pokryvností mladých stromů a keřů nad padlým kmenem a průměrem kmene. Druhově nejbohatší byly kmeny ve středních stadiích tlení II–III a zároveň silně kryté mladými stromy a keři a mající velký průměr, přičemž některé z nich byly nejbohatší ve srovnání s publikovanými pracemi. Druhové složení bylo významně ovlivněno jednotlivými stadii tlení, stupněm kontaktu kmene s půdou, průměrem kmene a pokryvností keřů a dospělých stromů. Vysoká pokryvnost mladých stromů a keřů byla doprovázena výskytem řady kornatců a drobných lupenatých hub, zjevně podporovaných vlhkým mikroklimatem pod pokryvem mladých stromů. 48 druhů bylo klasifikováno jako obecně vzácné nebo preferující přirozené lesy nebo spojené s boreálními/montánními ekosystémy. Nejzajímavější z nich, např. *Amylocystis lapponica*, *Antrodiella citrinella*, *Crustoderma dryinum*, *Fomitopsis rosea* a *Steccherinum gracile*, byly asociovány především s kmeny s nižším kontaktem s půdou. Funga mrtvého smrkového dřeva v Bělověžském pralese je velmi bohatá. Vyznačuje se výskytem některých extrémně vzácných druhů (*Cyphelloporia bialoviesensis*, *Gloeocystidiellum sibiricum*, *Mucronella pulchra*) a vzácných boreálních či boreálně-montánních prvků (*Asterodon ferruginosus*, *Boreostereum radiatum*, *Ceriporiopsis jelicii*, *Dichostereum boreale*, *Pycnoporellus alboluteus*, *Tricholomopsis sulphureoides*). K zachování stávající diverzity budou nutná opatření na globální i lokální úrovni.

INTRODUCTION

Białowieża virgin forest in Poland and Belarus is well-known as one of the largest and best-preserved natural forests in Europe (Faliński 1986, Keczyński 2017). It is a fungal diversity hotspot of international importance (e.g. Karasiński 2016, Ruszkiewicz-Michalska et al. 2021). Its crucial components are deadwood-inhabiting fungi associated with an unusually large number of different tree species. Due to recent climate change, bark beetle outbreaks and related human interventions, shifts in forest canopy composition and decrease of keystone tree species pedunculate oak (*Quercus robur*) and Norway spruce (*Picea abies*) are observed (Keczyński 2017, Boczoń et al. 2018, Kamińska et al. 2021). This could in the future threaten fungi and other organisms dependent on oak and spruce as a substrate.

Aware of this, we monitored macrofungi on 32 large decaying trunks of oak in 2016 (Holec et al. 2019a). Our intention was to use a uniform and well-established methodology to capture fungi inhabiting dead wood of formerly dominating but currently endangered tree species, especially for future comparisons. In 2017, we used the same methodology to study the fungi on spruce. After somewhat lengthy data processing due to organisational and practical reasons (e.g. the Covid pandemic in 2020–2023), we present the results here.

Our primary goal was to describe and analyse the richness and composition of fungal communities inhabiting fallen decaying trunks of spruce in relation to selected environmental variables to find out which of them are the most important. To put the results in a broader context, we compare the obtained data with works carried out following the same methodology in the Czech Republic (Holec et al. 2020, 2022, 2024a) as well as similar studies on biodiversity and ecology of fungi on spruce deadwood (for their reviews, see e.g. Heine et al. 2021, Runnel et al. 2021). The aim was also to compare the results from oak (Holec et al. 2019a) and spruce (this paper) to see if relevant ecological and mycodiversity patterns are similar or different.

MATERIAL AND METHODS

This study was conducted using basically the same approach as our previous research dealing with oak trunks (Holec et al. 2019a). Nevertheless, we describe here the most important data and procedures to make the article self-supporting.

Abbreviations. BNP: Białowieża National Park; BP33–BP64: codes of studied spruce trunks; CCA: canonical correspondence analysis; 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; GAM: generalised additive model; GLM: generalised linear model; GPS: global positioning system; HLI: heat load index; JB: Jan Běťák; JH: Jan Holec; JM: Jan Matouš; MB: Miroslav Beran; MCPT: Monte Carlo permutation test; MK: Martin Kříž; MKo: Monika Kolényová; N: north; PCA: principle component analysis; S: south; SSI: species of special interest; spec: number of fungal species on particular trunk studied; TK: Tomáš Kučera; W: west; I, II, III, IV, V: particular decay stages of studied trunks.

Study area. Northeastern Poland, Podlaskie Voivodeship, east of the town of Hajnówka, Białowieża National Park (Białowieski Park Narodowy), core zone of the BNP called 'strict reserve' (Keczyński 2017). Elevation 147–172 m a.s.l. Soils acidic to neutral, developed on Quaternary glacial deposits with a network of rivers and streams (Faliński 1986). The vegetation is represented by a lowland hemiboreal virgin forest minimally influenced by humans. Dominant trees 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 floodplain forests and bush. For details on environmental conditions see Faliński (1986), Keczyński (2017), and our previous summary (Holec et al. 2019a).

Climate and weather. 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. The precipitation in 2017 was slightly above the mean precipitation of the previous decade (706.14 mm), reaching 743.8 mm. This was due to the relatively high precipitation from February to April and in September, while the months May to August were drier than average. Temperature was slightly lower than the average for the previous decade. For data, see Electronic Supplement K.

Studied spruce trunks. The field work was carried out on 18–22 September 2017. Trunks of Norway spruce (*Picea abies*) were searched primarily in the peripheral areas of the BNP, for time-saving reasons. Vegetation around all the trunks was represented by the *Tilio-Carpinetum* association (based on vegetation samples by TK, in prep. for publication). We studied a total of 32 fallen trunks (Figs 1, 2) with diameters of 35–110 cm at breast height. Generally, care was taken to ensure (i) an even representation of trunks of different diameters and different decay stages and (ii) a mutual distance of at least 100 m. In most cases, the distance was more than 200 m. In several cases, forced by the impossibility of quickly finding a trunk of the required decay stage, trunks less than 100 m apart but differing by decay stage were also studied. Statistically, we conducted stratified random sampling within each subarea (block of trunks defined by area), ensuring that different categories of decay were represented in the block. This method helped control trunk diameter/decay variation and ensured that comparisons across categories were balanced.

The decay stage was estimated in accordance with the scale defined by Heilmann-Clausen (2001). Its key characters and the number of studied trunks are listed below:

I – fallen trunks without visible signs of decay, wood hard, bark intact (6 trunks, diameter 35–75 cm)

II – trunks with minor signs of decay, wood still rather hard, bark starting to break up (6 trunks, diameter 50–110 cm)

III – trunks with moderate signs of decay, surface wood distinctly softened, bark partly lost (8 trunks, diameter 45–110 cm)

IV – trunks with strong signs of decay but still with the ± original shape, surface wood strongly decayed, bark absent in most places (6 trunks, diameter 55–85 cm)

V – trunks rotten to almost humified, wood very strongly decayed, either to a very soft crumbly substance or to a flaky and fragile mass (6 trunks, diameter 50–70 cm).

In cases where decay was understood as a temporal successive process, we converted decay stages I–V to ordinal scale 1–5.

Trunk parameters were collected by JM, MKo, and TK (Electronic Supplements A, B) as follows: geographic position (coordinates measured with hand-held Garmin GPSmap 60CSx device with an accurracy ± 3–5 m), length of the lying part of the trunk (in analyses abbreviated to length), diameter at breast height (DBH), number of parts (parts), stump height if present (stump), decay stage (decay, see above), 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 in azimuth degrees (azimuth), canopy of mature trees (E3, %, 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 (E2, %, estimated as for E3), and total canopy cover (E3 + E2, abbreviated to E32, %). To assess trunk mass, we computed a derived parameter, based on DBH and length, namely trunk volume (volume).

Direct solar radiation on the studied trunks proved to be important in a previous study (Holec et al. 2019a). Therefore, we dealt with it in the same way (Holec et al. 2019a, modified from McCune 2007). Briefly, afternoon direct radiation was expressed by the gap folded aspect for SW orientation (causing the highest heat load index, $HLI = |180 - |azimuth - 225||$). The effects of slope and latitude were neglected due to their minimal variation.

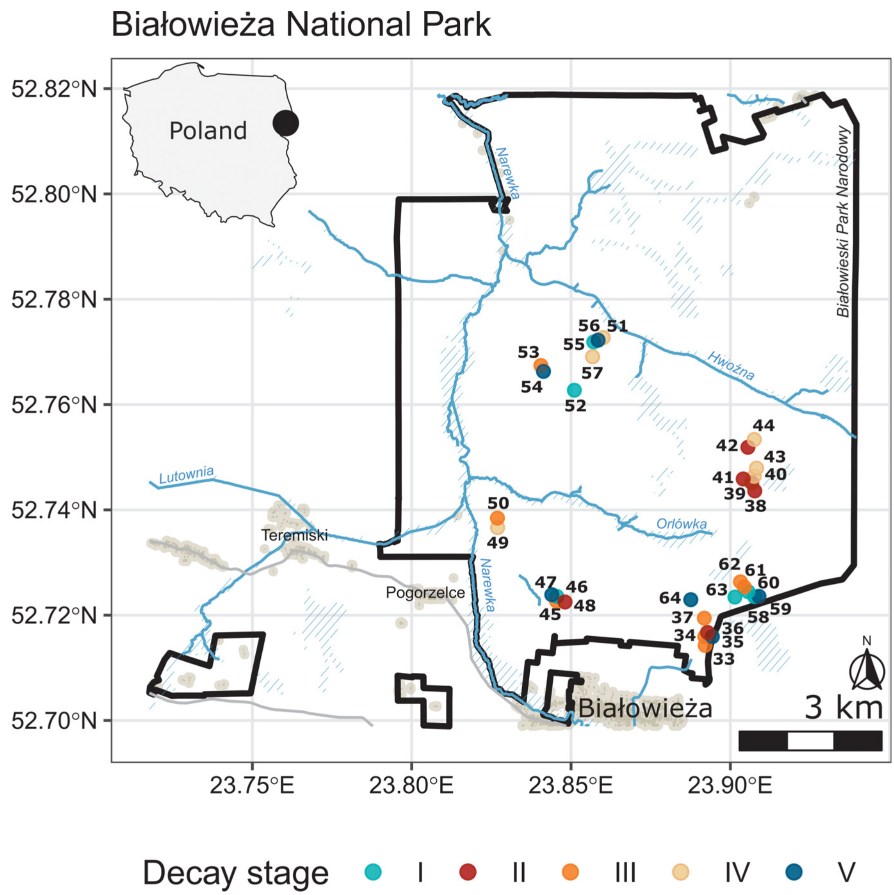


Fig. 1. Study area and position of studied trunks (BP33–BP64) of Norway spruce (*Picea abies*) in Białowieża National Park, Poland. For trunk data, see Electronic Supplements A, B. Map data are taken from OpenStreetMap. Prepared by M. Kolényová.

F u n g u s r e c o r d i n g. Fructification was notably high during our visit due to the heavy rainfall in September 2017 and the fact that temperatures were normal (not too high) during the summer (Electronic Supplement K). On each spruce 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 our previously published studies (see Introduction). 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, MB and MK. Vouchers are kept in herbaria PRM (mycological herbarium of the National Museum, Prague, collections of JH and MK), BRNU (Masaryk University, Brno, collections of DD), CB (Museum of South Bohemia, České Budějovice, collections of MB) and the private herbarium of JB. Records of some polypores were identified or revised by polypore specialist P. Vampola, collections of *Tomentella* by A. Jirsa (both Czech Republic). Taxonomy and nomenclature of most species follow Bernicchia & Gorjón (2010), Hansen & Knudsen (2000), Knudsen & Vesterholt (2012), Ryvarden & Gilbertson

Fig. 2. Examples of studied trunks of Norway spruce (*Picea abies*) in the strictly protected zone of Białowieża National Park, Poland. **a** – trunk in decay stage I (BP58); **b** – trunk in decay stage II (BP36); **c** – trunk in decay stage III (BP45); **d** – trunk in decay stage IV (BP57); **e** – trunk in decay stage V (BP47); **f** – most species-rich trunk BP53 (decay stage III) inhabited by 63 fungal species.

(1993, 1994), Ryvarden & Melo (2017), Wergen (2017, 2018), and Læssøe & Petersen (2019). *Corticiaceae* s.l. were identified according to Bernicchia & Gorjón (2010) and Larsson & Ryvarden (2021), with respect to The *Corticiaceae* of North Europe (Eriksson & Ryvarden 1973, 1975, 1976; Eriksson et al. 1978, 1981, 1984; Hjortstam et al. 1987, 1988). Recent taxonomic works on particular genera or groups published until 2023 were also consulted. In some cases, identification was only possible to the rank of genus (material too young, too old or damaged, or sterile). Uncertain identification of some taxa is expressed by abbreviations cf. (material very similar to the given species, but some characters slightly deviating) and aff. (material fitting into the given group, but differing significantly in some characters). Aggregates of (cryptic) species unrecognisable morphologically or unresolved taxonomically are indicated as agg. (e.g. *Tomentella sublilacina* agg.).

Species evaluation. Mycorrhizal status of individual species was taken from the above-mentioned identification literature and the UNITE database (unite.ut.ee). Scientific/ecological/conservation value of fungal species was assessed using the concept of 'species of special interest' (SSI; see Ódor et al. 2006 for definitions; Holec et al. 2024a, 2024b for selection of species). For the purposes of this paper, SSI include generally rare species, fungi preferring natural forests (for delimitation of natural forests, see Naturalforests.cz 2023, for summaries concerning fungal indicators of such forests, see Halme et al. 2017, Heilmann-Clausen et al. 2017), and fungi mainly associated with boreal and/or montane ecosystems. The Global Biodiversity Information Facility portal (GBIF: www.gbif.org) was consulted regarding the distribution of species. The fact if a species has been published from Białowieża National Park was verified in works by Karasiński et al. (2009, 2010), Karasiński & Wołkowycki (2015), Karasiński (2016), Holec et al. (2019), Kowalski et al. (2019), Gorczak et al. (2020), Kozłowska et al. (2022), Kujawa & Szczepkowski (2022), Kujawa et al. (2023), Yurchenko & Wołkowycki (2023), and lists of species published from the regular Exhibitions of Fungi of the Białowieża Forest by Gierczyk et al. (2013, 2014, 2015a, 2015b, 2017, 2018, 2019).

Data for comparison. We used data on macrofungi on fallen spruce trunks in the Bohemian Forest, Czech Republic (Holec et al. 2020, 2022, 2024a) and on fallen oaks in the Białowieża virgin forest (Holec et al. 2019a) obtained using the same methods. The only difference is that the works from the Czech Republic were based on four inspections of studied trunks during one season (spring, summer, autumn, late autumn), while the present work and our previous Białowieża study only contain data from the autumn visit. This is generally the richest wave of fungal fructification in Central Europe. For detailed comparisons we only used data from autumn visits.

Statistical evaluation.

Explanatory trunk and habitat variables. Since sampling was carried out in four subareas (see Studied spruce trunks and Fig. 1), we tested the effect of spatial distance of trunk positions (spatial autocorrelation) on the fungal species distance matrix using the Mantel test (Pearson's product-moment correlation, 999 permutations). The observed correlation between species and spatial distance matrices was very low (r = 0.04, p-level = 0.211) documenting that the matrices were independent. Then we checked for collinearity of separate variables by computing a matrix plot with Pearson's pair-wise correlations (Electronic Supplement D). Three groups of collinear parameters were detected: (i) those associated with decay, (ii) a canopy cover group (E3, E2, E32), and (iii) trunk dimension parameters. In subsequent analyses, these collinear groups were represented by their most significant variables.

Species richness. Species numbers were square-root transformed to achieve homogeneity of variances. Bartlett's test of variance homogeneity showed that the variances were not significantly different. For decay stages comparison, F tests in one-way ANOVA, followed by post-hoc Tukey's HSD comparisons, were used. Generalised linear modelling in R (R Core Team 2023) was used to assess the variables affecting fungal species richness. To improve the systematic part of GLM analysis and due to the non-linear response of residuals, we optimised non-parametric smooth term's complexity using generalised additive models (GAM, gam function, library mgcv; Wood 2017).

S p e c i e s c o m p o s i t i o n. Collinearity of centered and standardised explanatory trunk and habitat variables was inspected by means of principal component analysis (PCA). Groups of response variables were orthogonal (i.e. independent) and showed a pattern similar to the regression analysis (see above). Fungal species composition on the studied trunks was studied using gradient analyses in the Canoco 5.12 software (ter Braak & Šmilauer 2012, Šmilauer & Lepš 2014). As the relation between decay (expressed by an ordinal scale) and species composition on individual trunks was non-linear (similar to our previous studies, e.g. Holec et al. 2020), we additionally used particular decay stages (levels I–V). Unconstrained detrended correspondence analysis (DCA) of the total fungal species composition was used for the detection of the longest gradient expressed by the range of the first ordination axis. The total length of the largest distance measured by DCA was 4.93, which allowed us to use unimodal ordination methods. The relationship between species community pattern and trunk/habitat variables was tested within an unimodal constrained ordination framework (canonical correspondence analysis, CCA). Monte Carlo permutation tests (MCPT, number of permutations 4,999) with the forward selection procedure were used to select variables with the best fit of species data. Collinearity was avoided using adjusted p-values. In direct gradient analyses, singletons and doubletons (species found on only one or two trunks, respectively) were excluded.

Results

Fungal diversity

The total number of fungal occurrences on 32 trunks studied was 906. We recorded 272 species of macrofungi (Electronic Supplement C). Basidiomycetes were represented by 261 species, and macroscopic ascomycetes by 11 species belonging to the genera *Ascocoryne*, *Bertia*, *Camarops*, *Gyromitra*, *Helvella*, *Humaria*, *Hypocrea*, and *Protocrea*. The most species-rich genera were *Mycena* s.l. (28 species), *Tomentella* (10), *Botryobasidium* (8), *Cortinarius* s.l. (8), *Hyphoderma* s.l. (7), *Hyphodontia* s.l. (7), *Trechispora* (6), and *Galerina* (5). The most frequent species were *Galerina triscopa*, *Fomitopsis pinicola*, *Laccaria laccata*, and *Mycena stipata*, found on more than 50% of trunks. A total of 125 species (46%) were found on 1 trunk, and 46 species (17%) on 2 trunks only. Together, singletons and doubletons represented 63% of the total fungal diversity. Thus, the total funga consisted of a low number of frequent species and a high number of infrequent species, including many rarities (Tab. 1).

The most represented groups were gilled/boletoid fungi (109 species; 40%) and resupinate fungi (corticioids and resupinate heterobasidiomycetes: 93; 34%). Polypores, generally known as an ecologically important group of strong decayers, were represented by a relatively small number of species (37; 14%). Species with large basidiomata were above all *Fomitopsis pinicola*, *Physisporinus sanguinolentus*, *Fomitopsis rosea*, *Postia caesia* agg., *Antrodia serialis*, *Amylocystis lapponica*, *Heterobasidion annosum* agg., and *Phellinus nigrolimitatus* (in order of decreasing frequency).

Trunks in advanced decay stages (IV, V) were more frequently inhabited by mycorrhizal fungi, mostly gilled fungi and boletoids of the genera *Amanita*, *Cortinarius* s.l., *Hebeloma*, *Imleria*, *Laccaria*, *Lactarius*, *Naucoria*, *Paxillus*, *Russula*, *Xerocomellus*, further *Clavulina*, some resupinate fungi (*Amphinema*, *Piloderma*, *Pseudotomentella*, *Sebacina*, *Thanatephorus*, *Tomentella*, *Tylospora*), and ascomycetes (*Helvella*, *Humaria*). In total, 46 species of mycorrhizal fungi were found (17%).

Trunk parameters and fungal richness

Verification of the collinearity of individual trunk parameters (Electronic Supplement D) revealed three groups. Decay as the strongest variable was significantly positively correlated with trunk contact with soil (Pearson's correlation coefficient $r = 0.73$, significance value $p < 0.001$; being strongly correlated with moss cover; $r = 0.60$, $p < 0.001$), and negatively with bark cover ($r = -0.45$, $p < 0.01$). When additionally detected using PCA to show the correlation structure of the variables (Electronic Supplement F), the decay group was found to be associated with the second group consisting of vegetation cover parameters. The most important was total canopy cover (E32) as the sum of tree and shrub cover ($r = 0.94$, $p < 0.001$ and $r = 0.45$, $p < 0.01$, respectively). The third collinear group consisted of parameters associated with trunk dimension. The strongest one was diameter ($r = 0.56$, $p < 0.001$).

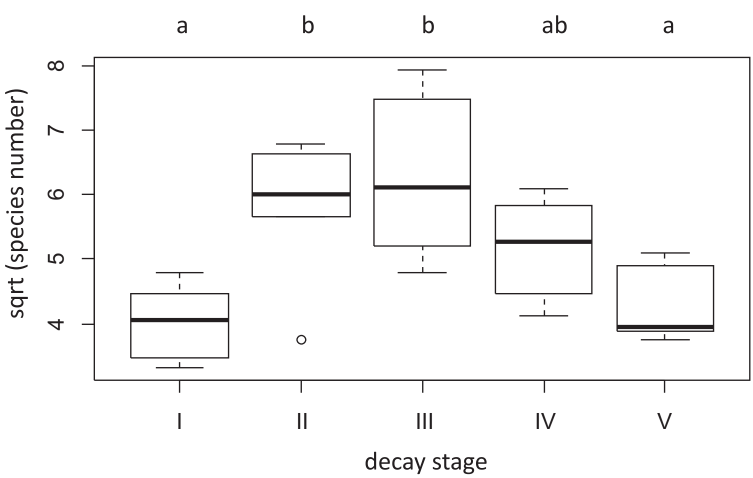


Fig. 3. Total number of species on trunks of decay stages I–V. Species number was square-root transformed (sqrt) to achieve homogeneity of variances required for the F test in one-way ANOVA followed by post-hoc Tukey's HSD comparisons. Letters indicate significantly different groups. Median, first and third quartiles, minimum/maximum values and outliers are visualised (for details, see Crawley 2013). For absolute values of the number of species, see Electronic Supplements C, E.

Individual trunks hosted 11 to 63 species of macrofungi (Electronic Supplement C) with an average number of 28 species per trunk. Trunks inhabited by the largest number of species were those of medium decay stages II–III but the slightly species-poor stage IV was not significantly different (Fig. 3). As shown in Electronic Supplement E, the highest species number was recorded in stage III (average 41, maximum 63). Initial stage I hosted only 11–23 species, terminal stage V 15–26 species. The number of fungal species on individual trunks was significantly positively correlated (Electronic Supplement D) with increasing shrub cover ($r = 0.69$, $p < 0.001$) and larger trunk diameters ($r = 0.54$, $p < 0.01$).

When analysed with regression modelling, the multiple explanatory variables were tested together by several models (GLM, GAM; Electronic Supplement H). The partial effects of decay and shrub cover on species richness were strong, both non-linear (decay) and linear (shrub), optimally explained by GAM (Fig. 4).

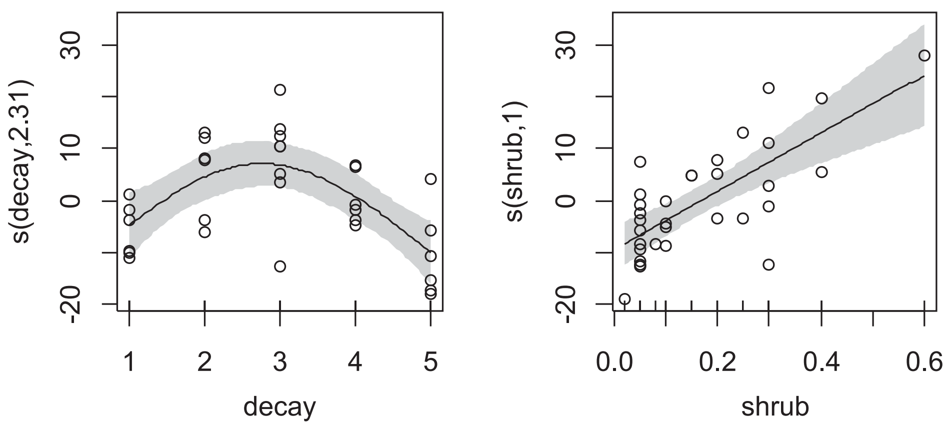
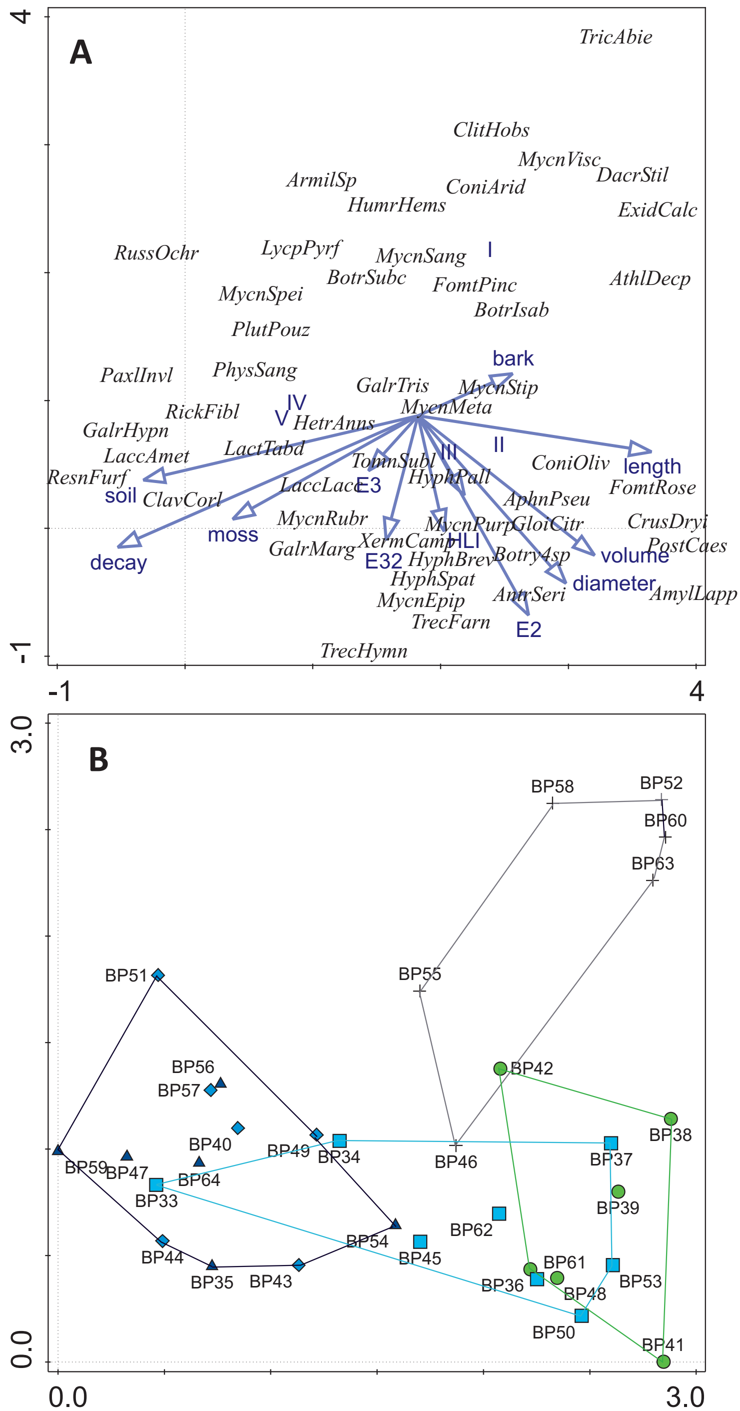


Fig. 4. Estimated smooth for species richness predicted by decay and shrub cover. The vertical axis shows the transformation functions for the GAM analysis. The model explains 70.4% of species richness variability. The horizontal axis covers (i) decay and (ii) shrub layer cover converted to a 0–1 scale. Partial residuals (circles) and approximate 95% pointwise confidence bands (in grey) are shown.

Fig. 5. Detrended correspondence analysis (DCA) of all fungal species on 32 trunks. First and second axes explain 14.1% of total species variation. **A** – Fifty fungal species with the highest weight and passively projected trunk and environmental parameters are shown. Individual decay stages are marked by Latin numerals I–V. For full names of fungi, see Electronic Supplement C, for abbreviations of parameters, see Material and methods. **B** – Centroid positions of individual trunks defined by their fungal assemblages (BP33–BP64) and marked according to decay stage (+: I, ○: II, □: III, ◇: IV, △: V). Trunks of the same decay stage are outlined (I: in grey; II: in green; III: in light blue; IV+V: in dark blue, the last two stages being framed together due to their large overlap). ►


A
B
TricAbie
ClitHobs
MycnVisc
DacrStil
ArmilSp
ConiArid
HumrHems
ExidCalc
RussOchr
LycpPyrf
MycnSang
I
BotrSubc
FomtPinc
AthlDecp
MycnSpei
BotrIsab
PlutPouz
bark
PaxlInvl
PhysSang
GalrTris
MycnStip
IV
MycnMeta
RickFibl
V
HetrAnns
GalrHypn
II
LactTabd
III
LaccAmet
TomnSubl
ConiOliv
length
ResnFurf
HyphPall
soil
ClavCorl
LaccLacc
E3
FomtRose
AphnPseu
MycnRubr
MycnPurp
GloiCitr
CrusDryi
moss
HLI
XermCamp
PostCaes
GalrMarg
volume
decay
E32
HyphBrev
Botry4sp
HyphSpat
diameter
AntrSeri
AmylLapp
MycnEpip
TrecFarn
E2
TrecHymn
4
-1
-1
4
3.0
0.0
0.0
3.0
BP58
BP52
BP60
BP63
BP55
BP51
BP42
BP56
BP57
BP38
BP40
BP49
BP34
BP46
BP37
BP59
BP47
BP64
BP33
BP39
BP62
BP54
BP45
BP44
BP61
BP36
BP53
BP35
BP43
BP48
BP50
BP41

Patterns of fungal species occurrence

The species composition of fungal assemblages on individual trunks together with the passively projected trunk/habitat parameters and individual decay stages are visualised in Fig. 5. The decay stages are positioned in different parts of the species pattern diagram (Fig. 5A). For further direct analyses, we therefore do not use a decay trajectory (Fig. 5A: decay arrow) but specific decay stages I–V, which better reflect the fungal assemblage pattern. The projection of individual trunks into the same space (defined by positions of their fungal assemblages) exhibits a similar pattern (Fig. 5B). Trunks of both stages I and II are separated from each other and from the overlapping stages IV and V, while stage III stands between them and partially overlaps them. In addition, the analogous figure in Electronic Supplement G shows that the bottom right parts of the diagrams cover the most species-rich trunks, namely those of decay stages II and III, simultaneously having the largest diameter and shrub cover.

Direct gradient analyses highlighted specialised species having a significant relationship to trunk parameters, specifically to the individual decay stages (Fig. 6), trunk contact with the soil, trunk dimension expressed by diameter, and the shrub cover (Fig. 7).

The decay stages are divided into three groups (Fig. 6). The clearly separated initial stage I is characterised by the presence of early colonisers *Exidia pithya*, *Trichaptum abietinum*, and *Peniophora pithya*. Stages II and III exhibit a high representation of species of special interest (SSI, see Tab. 1), e.g. *Amylocystis lapponica*, *Antrodiella citrinella*, *Crustoderma dryinum*, *Dichostereum boreale*, *Fomitopsis rosea*, *Steccherinum gracile*. The overlapping advanced stages IV and V are typical by many mycorrhizal fungi (e.g. *Cortinarius lignicola*, *Imleria badia*, *Laccaria amethystina*, *Lactarius quietus*, *Lactarius tabidus*, *Paxillus involutus*, *Russula ochroleuca*) and some wood-decayers, e.g. *Junghuhnia collabens* and *Phellinus nigrolimitatus*.

The effect of large trunk contact with the soil (which is collinear with decay) is especially visible in Fig. 7B. Except for mycorrhizal fungi (Fig. 6), such trunks (in decay stages IV or V) are typical for the presence of some corticioids (*Resinicium furfuraceum*, *Basidiodendron caesiocinereum*), small agarics (*Mycena speirea*, *Galerina hypnorum*, *Rickenella fibula*) and some polypores (*Physisporinus sanguinolentus*). Their opposite, i.e. trunks having little contact with the soil (raised by uprooted roots, protruding branches or other fallen trunks) are characterised by the SSI mentioned above (right parts of Figs 7A, 7B). High shrub cover (E2) is connected with a large number of corticioids and some small agarics (Fig. 7A: right lower quadrant). Some of the SSI also prefer this parameter, e.g *Antrodiella citrinella*, *Steccherinum gracile*, and *Dichostereum boreale* (Fig. 7B: right lower quadrant).

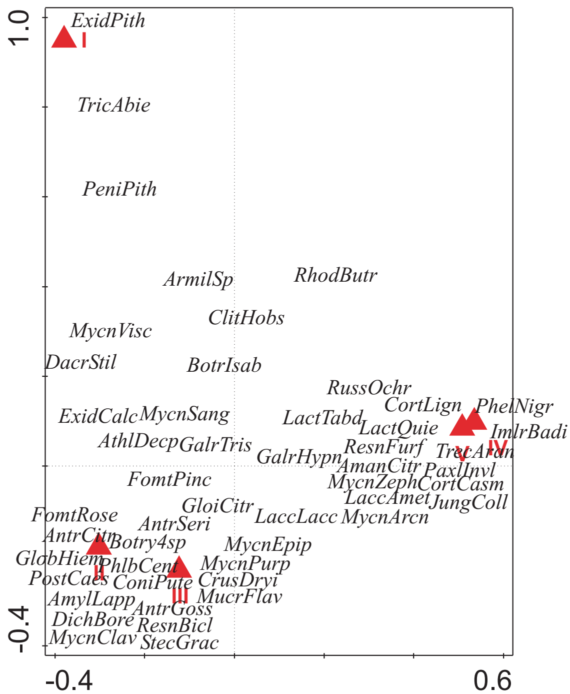
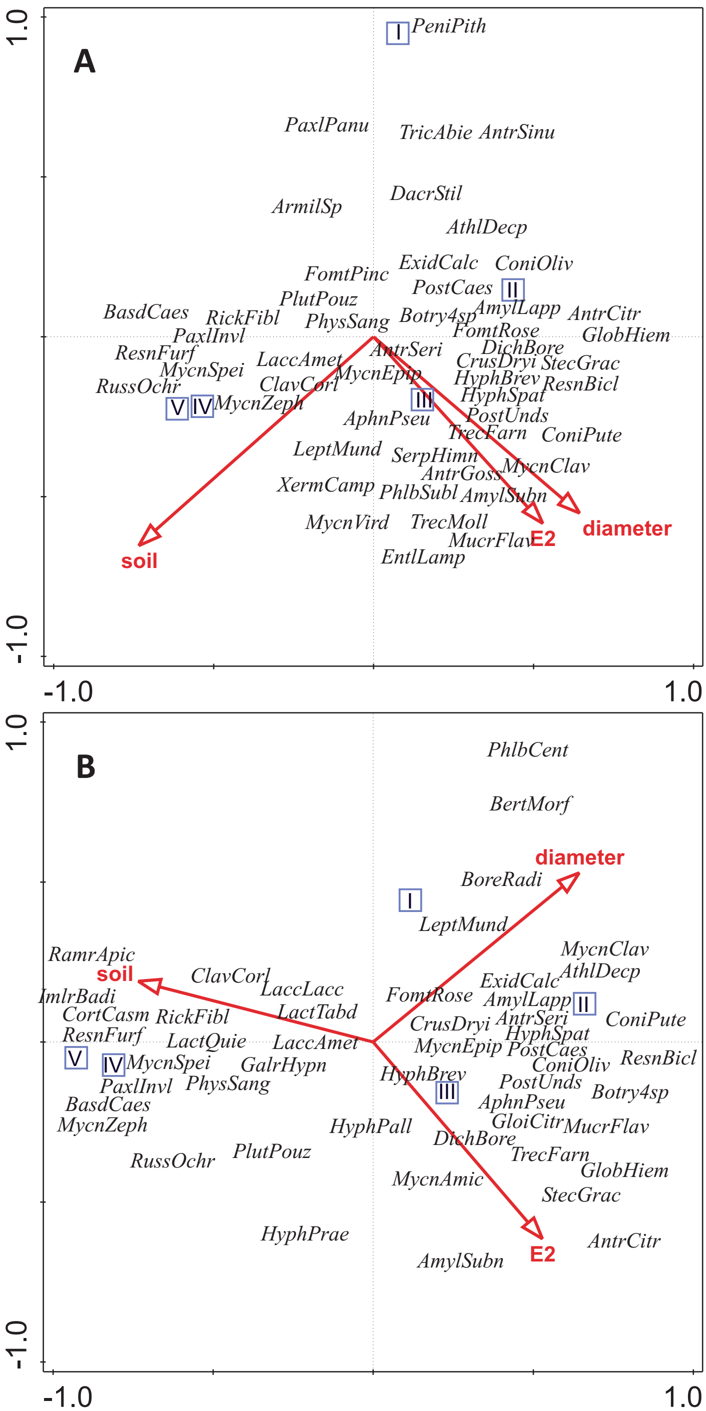


Fig. 6. Constrained analysis of fungal composition (CCA) with significant explanatory variable decay represented by individual decay stages (I–V). The decay stages explained 20.8% of total variance (F-ratio = 1.8, P(adjusted) = 0.001). The first two axes covered 15.0% of cumulative species variation. For full names of fungi, see Electronic Supplement C. Fifty species with the highest weight are projected.

DISCUSSION

Species richness in Białowieża and other localities

The number of 272 species recorded on 32 fallen spruce trunks during just one autumn visit in the Białowieża virgin forest represents a high fungal diversity. For comparison, only 168 species on 33 spruce trunks studied using the same methods were found during four visits (spring, summer, autumn, late autumn) in Boubínský prales virgin forest (Holec et al. 2020), the best preserved mixed montane forest of the Czech Republic (Holec et al. 2015). After adding data obtained later (Holec et al. 2022), 226 species are known from 36 spruce trunks at this site. Other studies are hardly comparable, as they were conducted in completely different habitats and using different methods, but also these show lower numbers of species. Just as an example, Renvall (1995) reported 120 species (basidiomycetes) on 320 spruce trunks with 0–14 species per trunk from northern


A
1.0
-1.0
-1.0
1.0
I
PeniPith
PaxlPanu
TricAbie AntrSinu
DacrStil
ArmilSp
AthlDecp
ExidCalc
ConiOliv
FomtPinc
PostCaes
II
PlutPouz
AmylLapp
BasdCaes
RickFibl
PhysSang
Botry4sp
AntrCitr
PaxlInvl
FomtRose
GlobHiem
ResnFurf
AntrSeri
DichBore
LaccAmet
CrusDryi
SteсGrac
MycnSpei
MycnEpip
HyphBrev
RussOchr
ClavCorl
ResnBicl
HyphSpat
V
IV
MycnZeph
III
PostUnds
AphnPseu
TrecFarn
ConiPute
LeptMund
SerpHimn
MycnClav
AntrGoss
XermCamp
PhlbSubl
AmylSubn
MycnVird
TrecMoll
diameter
MucrFlav
E2
soil
EntlLamp
B
1.0
-1.0
-1.0
1.0
PhlbCent
BertMorf
diameter
BoreRadi
I
LeptMund
MycnClav
RamrApic
AthlDecp
soil
ClavCorl
ExidCalc
LaccLacc
ImlrBadi
FomtRose
AmylLapp
II
CortCasm
RickFibl
LactTabd
AntrSeri
ConiPute
CrusDryi
ResnFurf
HyphSpat
LactQuie
LaccAmet
MycnEpip
PostCaes
V
ResnBicl
IV
MycnSpei
ConiOliv
GalrHypn
HyphBrev
PaxlInvl
PostUnds
PhysSang
Botry4sp
III
BasdCaes
AphnPseu
GloiCitr
MucrFlav
MycnZeph
HyphPall
DichBore
TrecFarn
RussOchr
PlutPouz
GlobHiem
MycnAmic
SteсGrac
HyphPrae
AntrCitr
AmylSubn
E2

◀ **Fig. 7.** Constrained analysis of fungal composition (CCA) with significant trunk parameters and passively projected decay stages. Fifty fungal species with the highest weight are projected. **A** – First (horizontal) and second (vertical) ordinal axes. **B** – First and third axes. The first three axes covered 16% of cumulative species variation. Contact with the soil explained 7.0% of total variance (F-ratio = 2.3, P-value < 0.001). Shrub (E2) explained 4.9% (F = 1.6, P = 0.002). Trunk diameter explained 4.1% [(F = 1.4, P = 0.026), P(adjusted) = 0.1]. The partial effects were for soil 7.7% (F = 2.3, P < 0.001) and for diameter 4.6% (F = 1.4, P = 0.027). The partial effect of shrub (E2, with soil and diameter as covariates) was non-significant. For full names of fungi, see Electronic Supplement C. For abbreviations, see Material and methods.

boreal primeval forests in Finland. Naturally, the trunks are thinner there and are poorer in species due to the harsh conditions. Lindblad (1998) reported 118 species on 108 trunks in Norway (one season, 2 visits).

Methodologically identical works from the Bohemian Forest in the Czech Republic (Holec et al. 2020, 2022, 2024a) were based on four trunk inspections per year. After comparing the results from the autumn inspection only, the trunks in Białowieża appear to be the richest in species (Fig. 8). We are aware of the fact that comparing lowland and mountain forests seems misleading, but if we use the same methodology and ask in which environment the diversity of fungi on spruce trunks is the highest, the comparison is legitimate. Of course, site specifics (e.g. different elevation, tree species composition, different species pool; discussed in next paragraphs) and the level of fructification during the years of study need to be considered carefully (see caption to Fig. 8).

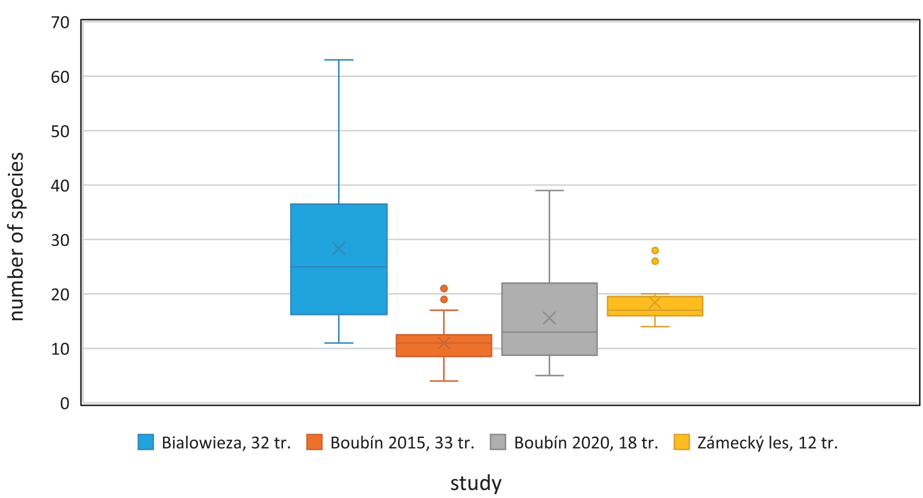


Fig. 8. Comparison of species richness on fallen spruce trunks during the autumn visit to Białowieża (this work: high fungal fructification) and the Bohemian Forest, Czechia (Boubín 2015: Holec et al. 2020, low fructification; Boubín 2020: Holec et al. 2022, high fructification; Zámecký les: Holec et al. 2024a, medium fructification). Explanations: box – interquartile range (3rd quartile – 1st quartile); line inside the box – median; x – mean value; lines above and undex the box – minimum, maximum (lowest and highest values excluding outliers), dots – outliers, tr. – trunk.

It is well known that in Central Europe, autumn is associated with the most species-rich wave of macrofungal fructification over the year. If we compare which percentage of species out of the total number of 4 visits per year is represented by the autumn visit alone (data from our previous studies: Holec et al. 2020, 2022, 2024a), we get to a range of 40–87% with a similar distribution of values at individual locations (Electronic Supplement I). The average value of this coefficient for all three sets of trunks is 63%. If we apply this minimalistically to the most species-rich trunks of Białowieża (55, 57, and 63 species, respectively, see Electronic Supplement B), they could host at least 70–80 species over the entire season, but possibly more. However, recent research in Boubínský prales (Kolényová et al. in prep.) suggests that the fungal species richness on local spruce trunks may be very similar to that of Białowieża. In that case, the collector effect (personal approach of each individual researcher) certainly plays a role, as the study by Kolényová et al. was conducted in an unusually thorough manner and with great emphasis on inconspicuous species like corticioids.

In conclusion, the fallen spruce trunks in Białowieża host very rich macrofungal communities, some trunks in medium decay stage III are the richest ones of all the studies discussed. This is probably first of all related to the extraordinary rich funga of the whole Białowieża virgin forest (Karasiński et al. 2009, 2010, Karasiński et Wołkowycki 2015, Karasiński 2016, Ruszkiewicz-Michalska et al. 2021). This mycodiversity hotspot of European importance represents a huge pool of spreading mycelia and spores of both common and rare species, including a large number of extreme rarities (Karasiński 2016, Karasiński et al. 2023). As shown by the cited authors, this is mainly associated with the large area of the site covered by old-growth forests (strict reserve of the BNP: 5,726 ha, entire Białowieża Forest World Heritage site in Poland and Belarus: 141,885 ha) and the continuous natural development of the strict reserve where no major human interventions have been carried out (Keczyński 2017). Ruszkiewicz-Michalska et al. (2021) reported 3,221 species of the Fungi kingdom from the Białowieża virgin forest (Polish part only), including 1,907 species of *Basidiomycota*, a group predominant in our dataset (261 species). Furthermore, small ascomycetes not recorded by us (e.g. *Mollisia*, *Orbilia*, non-stromatic pyrenomycetes, etc.) would further increase the number of known species overall. Spruce trunks in waterlogged habitats, not studied by us, possibly host also some other species. In addition, the transitional geographic position of Białowieża between boreal and temperate forests (expressed by the term 'hemiboreal forest') causes a mixing of species from two biogeographic zones. The low elevation is also important, considering the negative effect of increasing elevation on species richness of spruce deadwood (Holec et al. 2020). Due to all these facts, fungi in Białowieża are not exposed to climatic extremes (severe frosts, long-lasting snow cover, short vegetation season), which generally limit the occurrence of sensitive species in mountains or at high latitudes.

Trunk parameters and species richness

The high species richness was associated with medium decay stages II and III (Fig. 3), higher shrub cover (Fig. 4), and larger trunk diameter (Electronic Supplement D). The importance of decay stage and trunk diameter has already been demostrated before (e.g. Heilmann-Clausen & Christensen 2004, Juutilainen et al. 2011, Hofmeister et al. 2015, Runnel et al. 2021, Holec et al. 2020, 2022). It is generally known that species richness increases with area, here represented by trunk dimensions. We are aware of the fact that our most species-rich trunks are those of decay stages II and III, i.e. the categories in which thick trunks are most represented (Electronic Supplement B). However, the relation between decay stages and diameter proved to be non-significant (ANOVA, $F = 1.64$, $p = 0.19$). The richness of categories II and III is therefore not a reflection of a greater representation of thick trunks, but mainly their decay stage.

The role of shrub cover was stressed by Holec et al. (2020), also in a study on fungi of spruce deadwood. The positive effect of shading by the canopy of surrounding trees was highlighted by e.g. Lindblad (1998) and Kubartová et al. (2012). A possible explanation is the humid microclimate under the cover of shrubs and/or young trees, which at the same time reduces evaporation via a 'greenhouse effect' of their crowns. This probably supports the higher occurrence of climate-sensitive fungi like small agarics and corticioids.

In the case of Białowieża oaks (Holec et al. 2019a), orientation (azimuth) of the fallen trunks was significant instead of shrub cover. On sun-exposed oak trunks, the orientation of canopy gaps in the direction of the afternoon sun (a parameter called heat load, see Holec et al. 2019a) resulted in a lower fructification of fungi. This effect has not been demonstrated in spruce, probably because falling spruce crowns (which are slender) do not open up the canopy so much as wide oak crowns.

Patterns of fungal species occurrence

The key factors affecting fungal assemblages on individual trunks proved to be (i) decay with its collinear factors, especially trunk contact with the soil (correlated positively with decay) and bark cover (negatively), (ii) trunk dimension parameters, and (iii) shrub cover (Figs 5–7). The first two factors correspond with our results from the Bohemian Forest in Czechia (Holec et al. 2020, 2024a) and the classical study by Renvall (1995) from Finland. An interesting finding is that some rare species and fungi of natural forests (SSI) do not prefer the thickest trunks, but those with little contact with the soil (Fig. 7A). Such trunks can be both thin and thick and are in the earlier stages of decay, situated more or less elevated above the soil surface by still protruding, undecomposed branches or roots. Consequently, the interesting species should be sought not only on huge trunks lying on the soil, but also on thinner trunks in a position more or less above the ground.

During succession, which is best reflected by the gradient of decay stages, rather distinct fungal communities can be found in the initial (I), medium (II, III), and advanced (IV+V) stages (Figs 5, 6). However, it is clear that stage III overlaps with stages II and IV+V (Fig. 5B). Trunks of decay stage III have some parts, typically the bottoms or tops, in a lower or higher decay stage than their 'average' stage given in Electronic Supplement B. As a result, their fungal communities are enriched by species of earlier and advanced decay stages and are characterised by the presence of many SSI (lower left quadrant of Fig. 6, also listed in Results). These conclusions agree with those by Kolényová et al. (2024), who stressed that trunks in medium decay stages are morphologically more heterogeneous, offering different microhabitats for specialised fungi.

Interestingly, mycorrhizal fungi are already present on trunks in decay stage I (6 occurrences; data based on Electronic Supplement C). Their occurrence increases up to stage IV (II: 22, III: 40, IV: 56) and decreases in stage V (35). Generally, the frequent occurrence of mycorrhizal fungi on trunks in advanced decay stages is a well known fact (Kubartová et al. 2012, Mäkipää et al. 2017, Holec et al. 2020). Biologically, the mycorrhizal fungi are poor or no decayers. Their mycelium probably grows into the rotting wood from the surrounding soil. It is also possible that they find suitable conditions for fructification on strongly decayed wood which retains water well.

The history of tree fall and associated priority effects of initial inhabitants are known to be important for the species composition of fungi on discrete wood units (e.g. Ottosson et al. 2014, 2015; Holec & Kučera 2020). In our dataset, two ways of tree fall were represented, which was indicated by the number of trunk parts: either uprooting (1 part – complete fallen tree; 4 trunks) or breakage (2 parts – stump and fallen tree part; 28 trunks). However, their effect on fungal species composition proved to be insignificant, probably also due to the uneven representation of these two categories.

Comparison of fungi on wood of *Picea* and *Quercus*

We compared species found on oak trunks (Holec et al. 2019a) and spruce trunks (this study). The data in Electronic Supplement J shows that out of the more common species (inhabiting 10 trunks and more) some are specialists, while others occur on wood of both trees.

Picea only (in order of decreasing occurrence): *Fomitopsis pinicola*, *Mycena stipata*, *Exidiopsis calcea*, *Dacrymyces stillatus*, *Fomitopsis rosea*, *Mycena epipterygia*, *Coniophora arida*, *Postia caesia* agg.

Quercus only: *Hymenochaete rubiginosa*, *Phaeohelotium monticola*, *Xylobolus frustulatus*, *Mycena inclinata*, *Mycena galericulata*, *Gyrophanopsis polonensis*, *Laetiporus sulphureus*.

On oaks, we found a certain number of fungi preferring conifer wood (Holec et al. 2019a). Reversely, we also registered hardwood-preferring species on spruce wood, namely *Calocera cornea*, *Crepidotus variabilis*, *Hydropus floccipes*, *Hymenochaete cinnamomea*, *Hyphodontia crustosa*, *Hypholoma lateritium*, *Mycena arcangeliana*, and *Steccherinum ochraceum* (Electronic Supplement C). This is probably due to the co-occurrence of conifers and deciduous trees at the same locality and rich populations of fungi in Białowieża seeking out any usable substrate.

Red-list fungi, protected fungi, species of special interest (SSI), species new to BNP and Poland

We found 59 species (Electronic Supplement C) of the Red List of Fungi in Poland (Wojewoda & Ławrynowicz 2006), i.e. 22% of all species found, which is a high representation. Of these, 26 species are also included in the Czech red list (Zíbarová et al. 2024). Four of the species found (*Amylocystis lapponica*, *Fomitopsis rosea*, *Pycnoporellus alboluteus*, *Skeletocutis odora*) are also legally protected in Poland (Kujawa et al. 2020).

Red-list and protected species are sometimes chosen arbitrarily and only according to the local situation. Consequently, we also applied the SSI concept (for definitions and data sources, see Material and methods: Species evaluation), which takes into account general data on the distribution and ecology of the species. We also applied our long-time field experience from research at dozens of natural forest localities in Czechia, Slovakia, and Ukraine (Holec 2003, Holec 2008, Hofmeister et al. 2015, Adamčík et al. 2016, Dvořák et al. 2017, Šamonil et al. 2018, Holec et al. 2020, 2022, 2024a, Kolényová et al. 2024). Finally, 48 species (Tab. 1) can be classified as generally rare, preferring natural forests, or associated with boreal/montane ecosystems. These are the most valuable species we found on the studied spruce trunks. Of these, 25 are listed in the Polish red list and 37 in the Czech red list. Interestingly, a relatively significant portion of the SSI were captured not on just one, but several of the studied trunks (Tab. 1), e.g. *Fomitopsis rosea*: 12 trunks, *Crustoderma dryinum*: 9, *Amylocystis lapponica*: 6, *Dichostereum boreale*: 5, *Hydropus marginellus*: 5, *Mycena clavata*: 5. Only 19 of the 48 SSI were found just once. This demonstrates how rich the populations of otherwise rare species are in Białowieża. The most important species is *Cyphelloporia bialoviesensis* Karasiński, Holec & Dvořák, described as a genus and species new to science directly from the Białowieża virgin forest (Karasiński et al. 2023). Some of the original collections used to describe it were found on the trunks discussed here. Another locality of the species (not cited in Karasiński et al. 2023) is situated in the European part of Russia (Kilemary Nature Reserve near Nizhny Novgorod; Miettinen 2019).

In comparison with Boubínský prales, one of the best-preserved, spruce-containing montane virgin forests of Central Europe (Holec et al. 2015, 2024a, 2024b), Białowieża virgin forest is richer in the occurrence of some extremely rare species (*Cyphelloporia bialoviesensis*, *Gloeocystidiellum sibiricum*, *Mucronella pulchra*) and some boreal or boreal-montane elements (e.g. *Asterodon ferruginosus*, *Boreostereum radiatum*, *Ceriporiopsis jelicii*, *Dichostereum boreale*, *Pycnoporellus alboluteus*, *Tricholomopsis sulphureoides*). This is understandable, especially given the geographical location of Białowieża (hemiboreal forest) and its large area (discussed above).

Tab. 1. Most valuable species found on studied spruce trunks. Bor – species preferring boreal forests, Bor/Mont – boreal-montane species, CZ – Czechia, Mont – species occurring mainly in the mountains, Nat – species preferring natural forests (as defined in Naturalforests.cz 2023), Rar – generally rare species, SSI – species of special interest. For photographs of selected species, see Figs 9–22.

Species	No. of trunks	SSI (for delimitation, see Material and methods)	Czech red list (Zíbarová et al. 2024)	Polish red list (Wojewoda & Ławrynowicz 2006)
Amaurodon mustialaensis (P. Karst.) Kõljalg & K.H. Larss.	1	Rar	EN	
Amylocorticium canadense (Burt.) J. Erikss. & Weresub	2	Rar	unknown from CZ	
Amylocorticium cebennense (Bourdot) Pouzar	1	Nat	unknown from CZ	E
Amylocorticium subincarnatum (Peck) Pouzar	3	Nat	EN	E
Amylocystis lapponica (Romell) Singer	6	Nat, Bor/Mont	CR	E
Antrodia piceata Runnel, Spirin & Vlasák	1	Nat, Bor/Mont	CR	
Antrodiella citrinella Niemelä & Ryvarden	3	Nat, Bor/Mont	NT	E
Arrhenia epichysium (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	2	Nat	NT	V
Asterodon ferruginosus Pat.	1	Rar, Bor	unknown from CZ	E
Athelopsis subinconspicua (Litsch.) Jülich	2	Nat	VU	
Boreostereum radiatum (Peck) Parmasto	3	Rar, Bor (rarely also Mont)	CR	E
Botryobasidium medium J. Erikss.	4	Nat	NT	
Camarops tubulina (Alb. & Schwein.) Shear	2	Nat	NT	V
Ceriporiopsis jelicii (Tortić & A. David) Ryvarden & Gilb.	1	Nat, Bor/Mont	unknown from CZ	
Crepidotus kubickae Pilát	1	Nat		
Crustoderma dryinum (Berk. & M.A. Curtis) Parmasto	9	Nat	NT	E
Cyphelloporia bialoviesensis Karasiński, Holec & Dvořák	2	Rar, Nat	unknown from CZ	

Species	**No. of trunks**	**SSI (for delimitation, see Material and methods)**	**Czech red list (Zíbarová et al. 2024)**	**Polish red list (Wojewoda & Ławrynowicz 2006)**
Dacrymyces chrysospermus Berk. & M.A. Curtis	1	Nat	NT	V
Dichostereum boreale (Pouzar) Ginns & M.N.L. Lefebvre	5	Rar, Bor	unknown from CZ	
Fomitopsis rosea (Alb. & Schwein.) P. Karst.	12	Nat, Bor/Mont	EN	E
Gerronema xanthophyllum (Bres.) Norvell, Redhead & Ammirati	1	Rar	VU	R
Gloeocystidiellum sibiricum Parmasto	1	Rar, Bor	unknown from CZ	
Hydropus floccipes (Fr.) Singer	1	Rar	EN	
Hydropus marginellus (Pers.) Singer	5	Nat	VU	E
Hymenochaete fuliginosa (Pers.) Lév.	2	Nat, Bor/Mont	VU	E
Hyphoderma involutum (H.S. Jacks. & Dearden) Hjortstam & Ryvarden	1	Nat	EN	
Hyphodontia altaica Parmasto	1	Rar, Nat, Bor/Mont	CR	
Junghuhnia collabens (Fr.) Ryvarden	4	Nat, Bor/Mont	CR	E
Mucronella flava Corner	3	Nat	EN	
Mucronella pulchra Corner	1	Rar	unknown from CZ	
Mycena algeriensis Maire	2	Rar	VU	
Mycena clavata (Peck) Redhead	5	Rar	EN	
Mycena picta (Fr.) Harmaja	1	Rar	EN	E*
Ossicaulis lachnopus (Fr.) Contu	1	Nat	VU	
Phellinus ferrugineofuscus (P. Karst.) Bourdot & Galzin	2	Rar, Nat, Bor/Mont	CR	E
Phellinus nigrolimitatus (Romell) Bourdot & Galzin	4	Nat	VU	E
Phlebia subulata J. Erikss. & Hjortstam	3	Nat	VU	
Postia undosa (Peck) Jülich	5	Nat	NT	E
Pycnoporellus alboluteus (Ellis & Everh.) Kotl. & Pouzar	2	Rar, Nat, Bor/Mont	unknown from CZ	E
Rigidoporus crocatus (Pat.) Ryvarden	2	Nat	EN	E
Scytinostromella heterogenea (Bourdot & Galzin) Parmasto	2	Nat	VU	
Sidera lenis (P. Karst.) Miettinen	1	Rar, Bor	DD	V
Sidera vulgaris (Fr.) Miettinen	2	Nat	EN	
Skeletocutis odora (Sacc.) Ginns	2	Nat	EN	V
Skeletocutis stellae (Pilát) Jean Keller	1	Nat, Bor/Mont	EN	V
Steccherinum gracile (Pilát) Parmasto	4	Nat, Bor/Mont	EN	
Tricholomopsis sulphureoides (Peck) Singer**	1	Rar, Bor/Mont	unknown from CZ	
Tubulicrinis borealis J. Erikss.	1	Rar, Bor/Mont	VU	E

* as *Mycena concolor*

** collection and photograph from Białowieża published in Holec et al. (2019b)

Fig. 9. *Cyphelloporia bialoviesensis*, fallen trunk of *Picea abies* outside the set of monitored trunks, 13 Sep 2016 (JB16/355). Photo J. Běťák.

Fig. 10. *Cyphelloporia bialoviesensis*, fallen trunk of *Picea abies* outside the set of monitored trunks, 22 Sep 2017 (PRM 956593). Photo M. Kříž.

Fig. 11. *Boreostereum radiatum*, fallen trunk of *Picea abies* outside the set of monitored trunks, 19 Sep 2017 (PRM 946086). Photo J. Holec.

Fig. 12. *Boreostereum radiatum*, fallen trunk of *Picea abies* (BP41), 19 Sep 2017, not collected. Photo J. Běťák.

Fig. 13. *Gloeocystidiellum sibiricum*, fallen trunk of *Picea abies* outside the set of monitored trunks, 14 Sep 2016 (PRM 945214). Photo M. Kříž.

Fig. 14. *Mucronella pulchra*, fallen trunk of *Picea abies* outside the set of monitored trunks, 14 Sep 2016 (JB16/391). Photo M. Kříž.

Fig. 15. *Asterodon ferruginosus*, fallen trunk of *Picea abies* outside the set of monitored trunks, 21 Sep 2017 (BRNU DD BIA 17/273). Photo D. Dvořák.

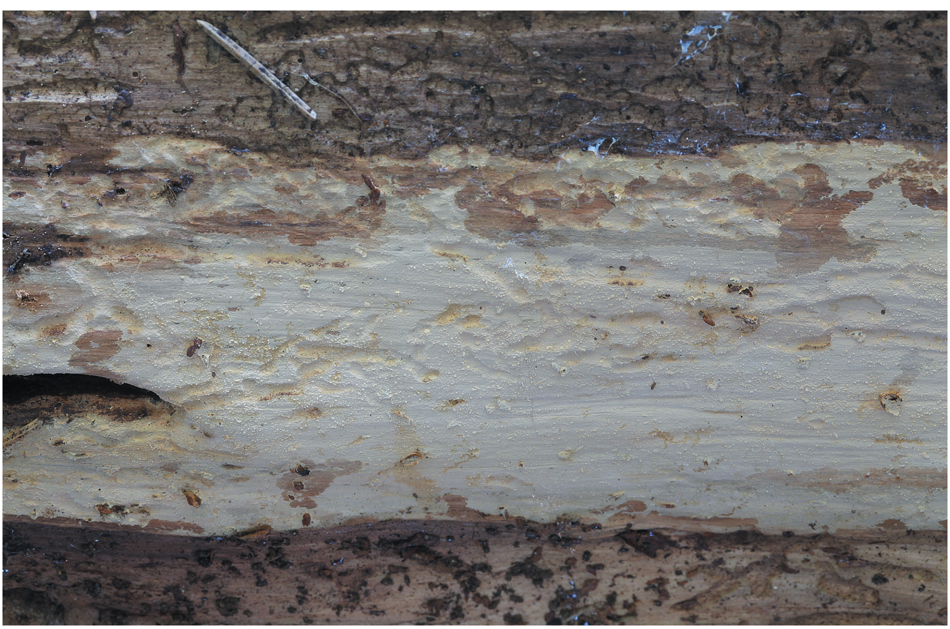


Fig. 16. *Dichostereum boreale*, fallen trunk of *Picea abies* outside the set of monitored trunks, 16 Sep 2016 (PRM 945190). Photo M. Kříž.

Fig. 17. *Pycnoporellus alboluteus*, fallen trunk of *Picea abies* outside the set of monitored trunks, 22 Sep 2017 (PRM 946108). Photo J. Holec.

Fig. 18. *Tricholomopsis sulphureoides*, fallen trunk of *Picea abies* outside the set of monitored trunks, 20 Sep 2017 (PRM 946095). Photo J. Holec.

Fig. 19. *Amylocystis lapponica*, fallen trunk of *Picea abies* (BP39), 19 Sep 2017 (PRM 946074). Photo J. Holec.

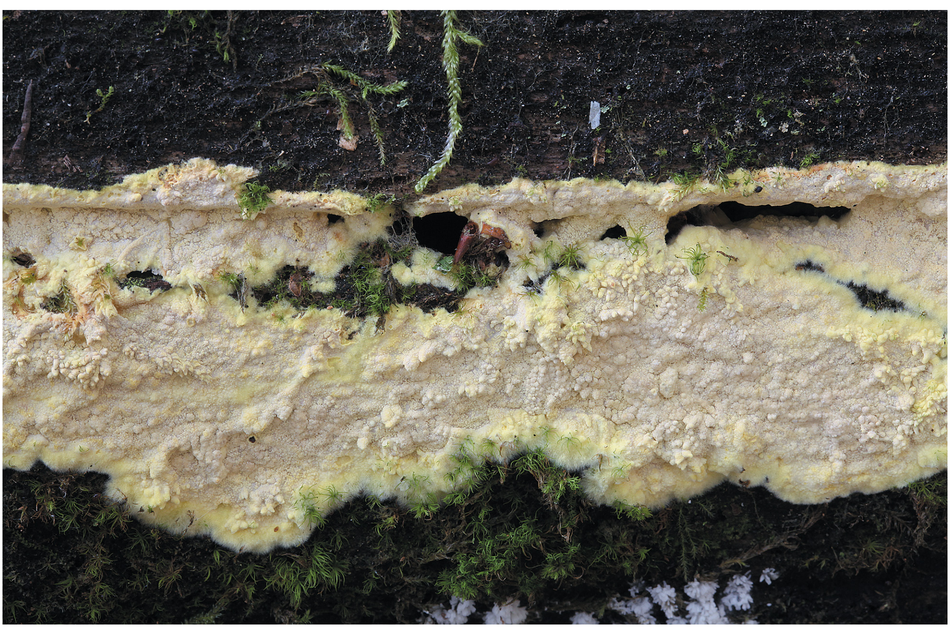


Fig. 20. *Amylocorticium subincarnatum*, fallen trunk of *Picea abies* outside the set of monitored trunks, 13 Sep 2016 (PRM 945342). Photo M. Kříž.

Fig. 21. *Antrodia piceata*, fallen trunk of *Picea abies* outside the set of monitored trunks, 19 Sep 2017 (BRNU DD BIA 17/12). Photo D. Dvořák.

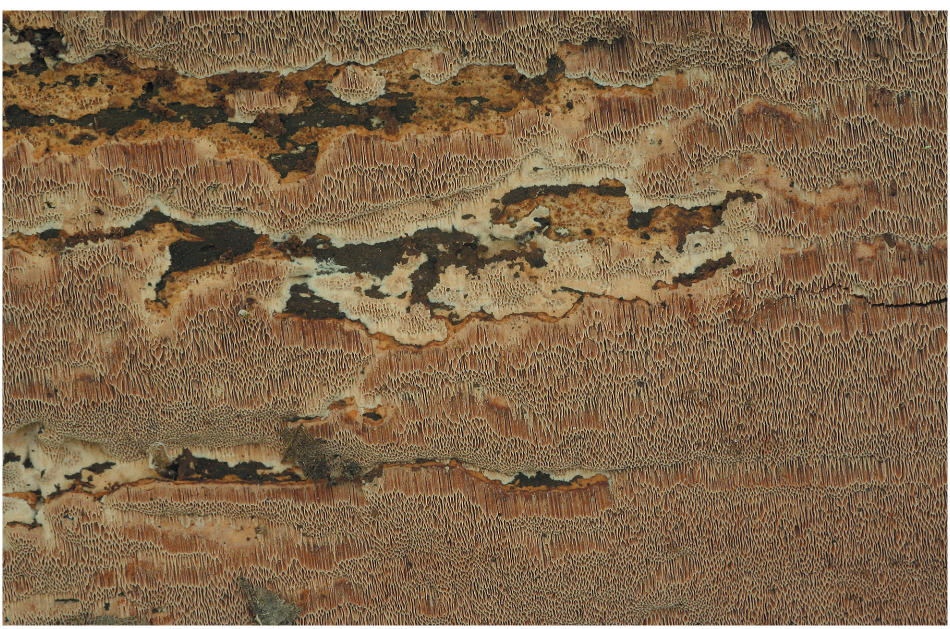


Fig. 22. *Junghuhnia collabens*, fallen trunk of *Picea abies* outside the set of monitored trunks, 13 Sep 2016 (BRNU DD 160913-09). Photo D. Dvořák.

In comparison with literature data on the funga of BNP (see Material and methods: Species evaluation), we recorded 30 previously unpublished species (Electronic Supplement C: species in bold). This is a relatively high number both absolutely and relatively (approximately every tenth species found was new to the BNP), especially considering the fact that only 32 trunks were studied. Most of them are fungi with inconspicuous fruitbodies like corticioids, tomentelloid fungi, heterobasidiomycetes, and small agarics. The detailed monitoring of discrete study units proved to be an effective way to capture them.

Four species are probably new to Poland (compare Kujawa et al. on-line), namely *Piloderma sphaerosporum*, *Protomerulius brachysporus*, *Tomentella pallidomarginata*, and *Xenosperma ludibundum*. Two other species provisionally idenfitied as *Leptosporomyces mundus* and *Repetobasidium erikssonii* are also absent from the cited list of macrofungi from Poland, but their identification will still need to be clarified, preferably molecularly.

Nature conservation prospects

Spruce in the BNP is threatened by increasing warming of the climate, associated outbreaks of bark beetles (e.g. Keczyński 2017, Boczoń et al. 2018, Kamińska et al. 2021) and subsequent human interventions in less protected parts of the forest (felling of infected and dead trees, deadwood removal). In the long term, there is a risk of spruce decline. This would then have a negative effect on fungi associated with spruce, whether as a host or a substrate. Our study showed that the funga of dead spruce wood in the Białowieża forest is enormously rich, perhaps even the richest in Europe. To preserve this richness, changes in human attitudes will be needed both at the global level (mitigating the impact of climate change) and at the local level (leaving a maximum amount of spruce wood in place, especially that of naturally dead trees, see Saine et al. 2023).

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