

Naturalness is key: high species richness of wood-inhabiting fungi does not automatically mean high species quality

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Diversity of wood-inhabiting macrofungi on large decaying trunks of Norway spruce and Silver fir was monitored in Zámecký les near-natural forest in Czechia. The aim was to statistically evaluate the fungal species richness and composition in relation to environmental/trunk parameters and to compare it with data on forest naturalness taken from historical documents. The results were compared with data obtained by the same methods in Boubínský prales virgin forest and literature data from Mittelsteighütte natural forest. Surprisingly, trunks in the near-natural forest were species-richer than in the virgin one, showing that the available ecological niche, here a fallen trunk, can be occupied by a rich set of fungi regardless of human impact. However, species composition differed considerably among the sites, especially by the presence of rare, red-listed and old-growth forest fungi, designated as species of special interest (SSI). They were least represented in the near-natural forest, more in the natural forest, and most in the virgin forest. This correlation shows that the independent concepts of both SSI species and classification of forest naturalness go well together. Even seemingly small interventions in the past like selective cutting have a big impact on fungal communities. The most sensitive fungi like *Amylocystis lapponica*, *Fomitopsis rosea* or *Phellinus ferrugineofuscus* require unbroken forest continuity. They are absent from affected sites although their refugia as potential sources of propagules exist nearby. Our data document that only spruces and firs 500–600 years old indicate true forest continuity. Linking fungal occurrence data, environmental variables and historical documents on human interventions is crucial both for understanding ecosystem processes and conservation management.

Key words: Central Europe, Bohemian Forest, mixed montane forests, ecology, spread limitations.

Human pressure on the landscape, including forests, is constantly increasing. Mycologists are worried about its effect on diversity and composition of fungal communities in forests (Bengtsson et al. 2000, Lindner et al. 2006, Paillet et al. 2010, Blaser et al. 2013, Abrego & Salcedo 2013, Brazeo et al. 2014, Heilmann-Clausen et al. 2014, Juutilainen et al. 2014, Purahong et al. 2014, Goldmann et al. 2015, de Groot et al. 2016, Suominen et al. 2019, Tomao et al. 2020, Heine et al. 2021). This applies in particular to wood-inhabiting fungi which lose their substrate by removing living and dead trees (Müller et al. 2007) and suffer from habitat changes connected with silvicultural practices (Bässler et al. 2010). Wood-inhabiting (lignicolous) fungi, functioning ecologically as endophytes, parasites, and decomposers, are ideal model groups, which enables answering general questions on species diversity, com-

munity ecology and conservation biology (Heilmann-Clausen & Christensen 2004; Küffer et al. 2008; Kubartová et al. 2012; Norros et al. 2012; Rajala et al. 2012, 2015; Abrego & Salcedo 2013; Ottosson et al. 2014, 2015; Hoppe et al. 2016; Juutilainen et al. 2017; Komonen & Müller 2018; Purhonen et al. 2019; Holec & Kučera 2020; Holec et al. 2020, 2022a; Moor et al. 2020; Nordén et al. 2020; Runnel et al. 2021; Abrego 2022; Rustøen et al. 2023).

Various studies have documented a reduction of the diversity of wood-inhabiting fungi in forests and a shift in their community composition caused mainly by these factors: clearcutting and selective logging (Bader et al. 1995, Lindblad 1998, Josefsson 2010), intensive thinning (Müller et al. 2007), salvage logging after insect outbreaks (Bässler et al. 2012), forest fragmentation (Abrego & Salcedo 2014, Grilli et al. 2017) and canopy gaps formation

(e.g. Perreault et al. 2023). Tomao et al. (2020) concluded that the higher is the forest management intensity the lower is the diversity of ectomycorrhizal and wood-inhabiting species, at least in the short term. Thus, the forest naturalness reflecting the degree of human interventions is a key factor determining especially the presence of endangered lignicolous species (Junninen et al. 2006). Some of them proved to be good indicators of forest naturalness (Bader et al. 1995, Kotiranta & Niemelä 1996, Parmasto 2001, Holec 2003, Christensen et al. 2004, Müller et al. 2007, Blaschke et al. 2009, Dvořák et al. 2017, Halme et al. 2017, Heilmann-Clausen et al. 2017). Presence of such fungi as well as high total

mycodiversity is connected above all with the large forest size and tree cover continuity, plus rich presence and diversity of deadwood, especially of the huge living trees and big units of the coarse wood debris (CWD) (Paillet et al. 2010, Hofmeister et al. 2015, Ruokolainen et al. 2018, Runnel et al. 2021, Majdanová et al. 2023).

Although our knowledge of these phenomena is growing, it is surprising that studies on the impact of forest management on wood-inhabiting fungi rarely specify exact character and intensity of human impact. In most publications, only brief and vague information is given, such as „selectively logged in the past, partially deforested in the 19th

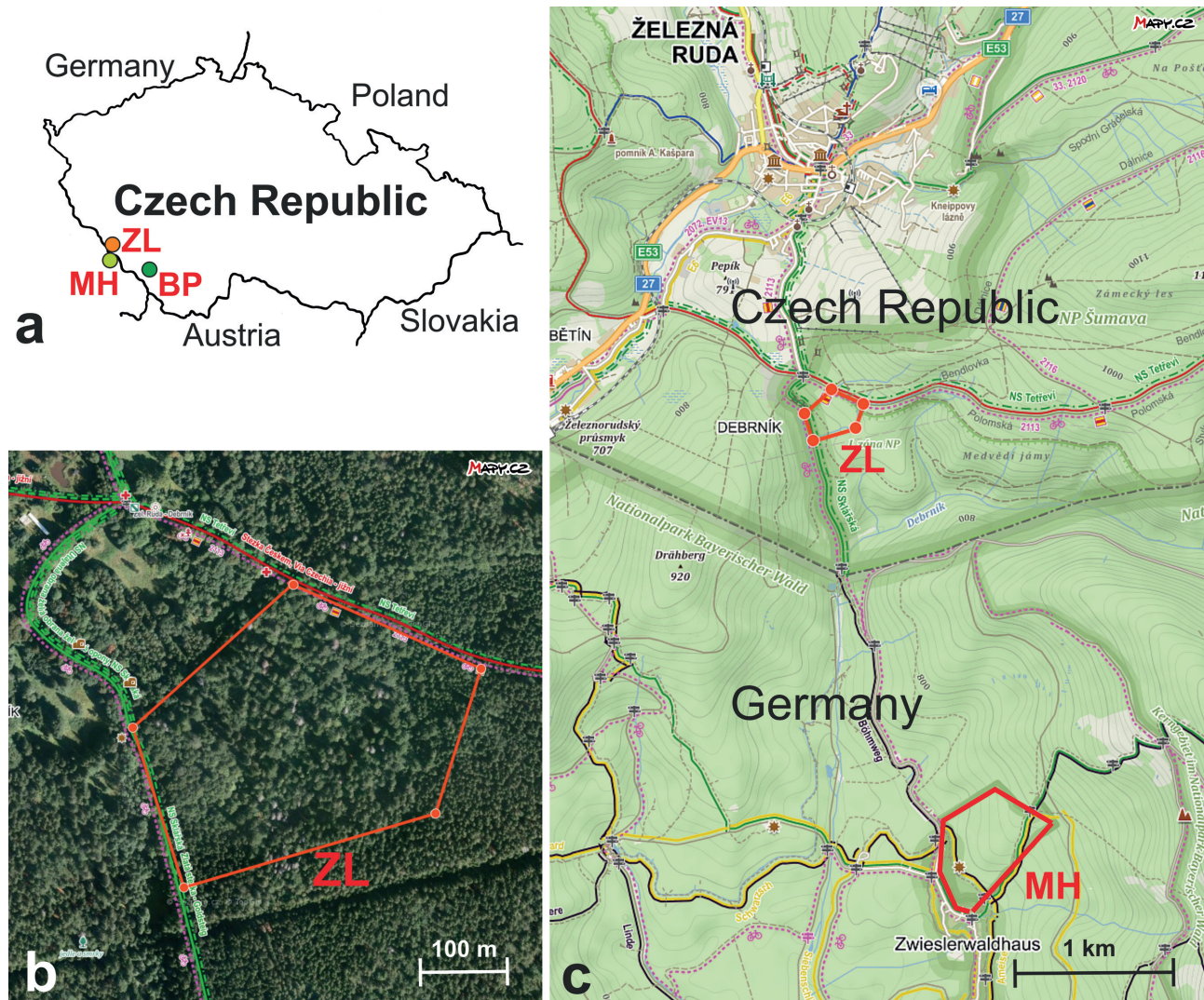


Fig. 1. Geographic location of the Zámecký les forest (ZL) and the localities used for comparison: Boubínský prales (BP) and Mittelsteighütte (MH). In figure b, notice the difference between the forest composition at the Zámecký les (large old trees, heterogeneous structure of the near-natural forest) and its surroundings towards the east and south (young trees, homogeneous structure of the man-made forest). Source of basic maps: Mapy.cz (www.mapy.cz), @Seznam.cz, a.s., 2023.

century“ etc. As indirect evidence of forest continuity and past interventions, the number of cut stumps per hectare was used by Bader et al. (1995) and tree age structure plus representation of oldest trees based on dendrochronology by Josefsson (2010) and Majdanová et al. (2023).

We decided to use historical documents to specify the time and type of human interventions in forest stands of different naturalness. As a „virgin forest stand“, we used Boubínský prales in Czechia, located in the Bohemian Forest Mts. (Vrška et al. 2012, Holec et al. 2015). We compared it with similarly looking stand in the same mountain range – Zámecký les forest near the village of Železná Ruda (Fig. 1). It is remarkable by multi-aged structure with numerous huge individuals of spruce and fir, both living and dead, having a diameter of up to 130 cm, height up to 50 m and age up to 280 years. Just visually, the stand looks like a virgin forest (Fig. 2). However, it was significantly influenced by man in the past (Electronic Supplement A) as it was adjacent to the former Debrník chateau (Schloss Deffernik, built in 1779, demolished in 1989) belonging to glassmaking families (Fig. 3a). They used wood from surrounding forests for their glassworks already since 1774 and especially in the 19th century. Moreover, big and slowly decaying stumps after felling of large spruces and firs in the second half of the 20th century are still visible, documenting selective cutting in not too distant history.



Fig. 2. Forest interior. **a.** Zámecký les forest (near-natural forest), **b.** Mittelsteighütte (natural forest), **c.** Boubínský prales (virgin forest).

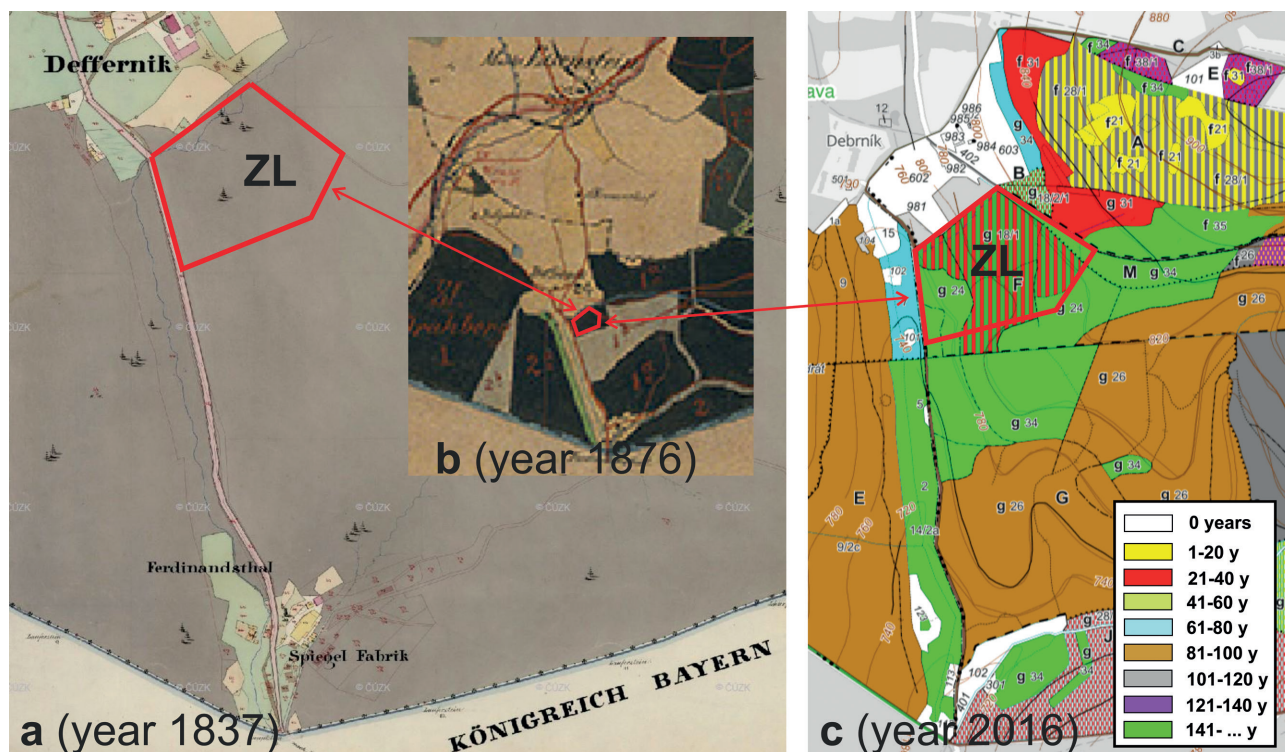


Fig. 3. Forest history at Zámecký les (ZL) documented by cadastre and forestry maps. **a.** State in 1837, original map of the stable cadastre. @ State Administration of Land Surveying and Cadastre of the Czech Republic, Archival maps, https://ags.cuzk.cz/archiv/openmap.html?typ=omc&idrastru=B2_a_4C_1122_6. Note the continuous forest (in grey) between the former Deffernik chateau and the former mirror factory (Spiegel Fabrik) in the Ferdinandsthal valley. **b.** State in 1876, archival forestry map, taken from Hubený (2023). The dark green colour of the ZL and some of the surrounding stands indicates forests older than 100 years, the grey colour of stands up to 20 years old. Note that the stands to the east and south of the ZL have been cleared shortly before 1876. **c.** State in 2016, current forestry map. Taken from Lesní hospodářská kniha (Forest management book), LHC 382216 – ÚP Prášily, 01.01.2016 – 31.12.2027 (depon. in Forests of the Czech Republic, state enterprise). The ZL stand having green colour is about 200 years old (average value, estimation) and red hatching indicates the existence of undergrowth with an age of around 40 years (composed mostly of beech).

We hypothesized that due to the aforementioned human interventions, the fallen decaying trunks in Zámecký les are species-poorer and less valuable in terms of the representation of rare, threatened and bioindicator species that in the Boubínský prales virgin forest. On the other hand, the Zámecký les mycobiota could have been re-enriched via propagules from a nearby refugium, the Mittelsteighütte nature reserve in the Bavarian Forest National Park, Germany. It is a very valuable natural forest of the similar tree composition and elevation like Zámecký les, located only 3.5 km away on the same-oriented slope in the Grosse Deffernik stream valley. Its rich and rare mycobiota is well known (Nuss 1999, DGfM 2023) and suitable for comparison.

Our questions were: 1. if the wood-inhabiting mycobiota of a stand that looks like a virgin forest, but has been principally affected by man (Zámecký les), is as species-rich and valuable like in the true

virgin forest (Boubínský prales) and the nearby natural forest (Mittelsteighütte); 2. what are the main factors responsible for possible differences.

Materials and methods

Study site Zámecký les and the localities compared

All sites (see below) are located in the same mountain range, namely the Bohemian Forest on the border between the Czech Republic and Germany (Fig. 1). Data on their habitat conditions and forest history are summarized in Electronic Suppl. A. Vegetation of all sites is very similar and made up of herb-rich beech forest with a significant proportion of Norway spruce (*Picea abies*) and Silver fir (*Abies alba*) (Fig. 2). The classification of forest naturalness in Zámecký les, Boubínský prales and their surroundings was taken from the Czech Natural Forests Databank (<https://naturalforests.cz/>

czech-natural-forests-databank) under names Boubínský prales and NP Šumava - Medvědí jámy - Pod Sklářským vrchem. Data on Mittelsteighütte were taken from Nuss (1999) and classified according to the Proposal for terminology standardization at web page Naturalforests.cz (2023). In this document, three categories of the broadly conceived term natural forest (= old-growth forest) are recognized based on level of human interventions: 1. virgin (original) forest, 2. natural forest, 3. near-natural forest.

Zámecký les (ZL), near-natural forest (Figs. 2a, 3)

Czech Republic, located in the Bohemian Forest (= Šumava) National Park (NP), 1.6 km S of the village of Železná Ruda, site called Debrník (after former Debrník = Deffernik chateau), forest stand called „Zámecký les“, natural zone of the NP, elevation 770–825 m a.s.l., coordinates of the centre 49.1230436N, 13.2352622E, area ± 8 ha, mixed montane forest (*Fagus sylvatica*: mostly younger and middle-aged trees; *Picea abies* and *Abies alba*: mostly large old trees) with multi-aged structure and high amount of coarse wood debris, habitat: herb-rich beech forest = *Asperulo-Fagetum* beech forest (Chytrý et al. 2010, AOPK ČR 2023). Data regarding human impact were obtained by P. Hubený from cadastre maps, historical and forestry archives (Fig. 3) and by J. Holec from the web site on glassworks in Debrník area (<http://m.taggmanager.cz/trail/cs/122>). In short, the stand is a man-influenced successor of the original virgin forest currently surrounded by young and middle-aged managed spruce forests. Its complete deforestation was probably not permitted by the owners of the nearby Debrník chateau and glasswork (see Introduction).

Boubínský prales (BP), virgin forest (Fig. 2c)

Czech Republic, located in the Bohemian Forest (= Šumava) Protected Landscape Area. Habitat data were taken from Vrška et al. (2012) and Holec et al. (2015, 2020). The site is protected as a national nature reserve. It is a perfectly preserved original forest never affected by forestry interventions, very valuable even from a pan-European perspective.

Mittelsteighütte (MH), natural forest (Fig. 2b)

Germany, located in the Bavarian Forest National Park (= Nationalpark Bayerischer Wald), formerly protected as a nature reserve, now a strictly protected area („Urwaldgebiet“) inside the national park. Habitat data were taken from Nuss (1999). It

is a natural forest minimally affected by humans (selective cutting of individual trees in period 1850–1914, see Electronic Suppl. A).

Studied trunks and their characteristics

The largest fallen trunks present in ZL were selected to be comparable with those from BP studied earlier and used here for comparison (Holec et al. 2020, Holec & Kučera 2020, Holec et al. 2022a). Their diameter at breast height was 90–130 cm for *Picea* and 85–115 cm for *Abies* (Electronic Suppl. C, D). As the number of such trunks was very limited, only 12 trunks of *Picea* (coded DP) and 6 of *Abies* (DA) could be selected (Electronic Suppl. B), covering all decay stages more or less equally. Their characteristics were recorded by J. Holec in August 2022 (Electronic Suppl. C, D): way of fall (broken or uprooted), diameter at breast height (DBH, in cm), length (m), geographic coordinates (using handheld Garmin GPSmap 60CSx device), direction of fall (in azimuth degrees), elevation (m a.s.l.), decay stage (1–5, average value for the entire trunk; estimated in accordance with Heilmann-Clausen 2001 and Holec et al. 2015, 2020), contact with the soil (%), bark cover (%), moss cover (%), cover of trees (E3, %, estimated from a rectangle covering the trunk and 1 m more at both sides), cover of shrubs and young trees up to a height of 5 m (E2, %, estimated like E3), total canopy cover (E32, %). Trunk volume was calculated according to the formula for a truncated cone using $\frac{1}{2}$ of the DBH as radius of the bottom disc and 2.5 cm as radius of the top disc (resulting from 5 cm as the usual width of the fallen trunk top). The trunk DA07 was represented only by its lower half having a diameter of the top disc 50 cm. In this case, 25 cm was used as radius of the top disc.

Monitoring of fungi in Zámecký les

Four mycological inspections were conducted on each trunk in ZL in 2021–2022, always at the time of the greatest fructification for the given period (spring visit: 15–16 June 2021, summer: 9–10 August 2021, late autumn: 15–16 November 2021, autumn: 29–30 September 2022). All visible macromycetes were recorded. For comparability, the field work and elaboration of fungal records was done in the same way as during our previous studies in Boubínský prales (Holec et al. 2020, 2022a; Holec & Kučera 2020). All fungi were recorded and identified by J. Holec. Most collections of polypores were revised by P. Vampola (Smrčná, Czechia), some collections of tomentelloid fungi by A. Jirsa (University of South

Bohemia, Czechia). Vouchers of hardly identifiable taxa are deposited in the mycological herbarium of the National Museum, Prague (PRM 957149–957282, 959002–959099).

Data for comparison

Data from trunks monitored in BP by the same methods like in ZL were taken from our previous publications: 18 trunks of *Picea* studied in 2020 (Holec et al. 2022a) and 30 trunks of *Abies* studied in 2017–2019 (Holec & Kučera 2020), see Electronic Suppl. C, D (trunk characteristics) and Electronic Suppl. F, G (fungal occurrence data). In some cases, data from 33 trunks of *Picea* studied in 2015 (Holec et al. 2020) were also consulted. Data on fungi occurring in MH were taken from Nuss (1999) and DGfM database (DGfM 2023).

Species of special interest (SSI)

Threatened species included in the Czech Red List (Holec & Beran 2006), generally rare species and fungi preferring old-growth forests were classified as “species of special interest” (SSI). For the general concept of the SSI see e.g. Ódor et al. (2006). For selection of the old-growth forests species, see relevant references in introduction and the following publications focused on individual species: Antonín et al. (2011), Běťák et al. (2012, 2021), Holec & Kolařík (2017), Holec & Zehnálek (2021), Holec et al. (2019, 2022b, 2023), Vampola (2021), Langer et al. (2022).

Statistical evaluation

Explanatory trunk and habitat variables. Similarly to our previous studies (Holec et al. 2020, Holec & Kučera 2020), all explanatory variables were inspected for multicollinearity using principal component analysis (PCA, see Electronic Suppl. E). One group of the collinear trunk variables was represented by the bark cover (Bark), which was negatively correlated with decay stage (Decay, Pearson’s correlation coefficient $r = -0.72$, $p < 0.001$), total canopy cover (E32, $r = -0.53$, $p < 0.001$) and moss cover (Moss; $r = -0.50$, $p < 0.001$). Decay covered positively also the moss cover ($r = 0.61$, $p < 0.001$), trunk contact with soil (Soil; $r = 0.57$, $p < 0.001$) and the total canopy cover ($r = 0.51$, $p < 0.001$). Trunk dimension parameters were best represented by volume (Volume) being collinear with trunk length (Length; $r = 0.52$, $p < 0.001$) and the trunk diameter (DBH; $r = 0.78$, $p < 0.001$). On the other hand, the trunk length was negatively correlated with decay

stage ($r = -0.49$, $p = 0.001$). Of the trunk dimension parameters, only length had partial significant effect on species richness (N_{spec} , $r = 0.40$, $p < 0.001$). The total fungal species richness was tested to partial effect of locality and tree species using nested ANOVA. The canopy cover group of variables (E3, E2, E32) was best expressed by common effect of the trees and shrubs (E32), representing also the partial effects of both tree (E3; $r = 0.70$, $p < 0.001$) and shrub cover (E2; $r = 0.28$, $p = 0.03$), respectively. Nevertheless, the tree and shrub covers were related negatively with each other ($r = -0.34$, $p = 0.005$). The moss cover had significant relation to the total canopy cover ($r = 0.46$, $p < 0.001$). The folded aspect of fallen trunk to south-west (FAsw), expressing its exposure to afternoon sun (and, thus, its drying out), was computed as described in Holec et al. (2019). As insignificant, it was not used in subsequent analyses.

Due to the high multicollinearity of the above mentioned explanatory variables (Electronic Suppl. E: right figure), we counted substitute variables derived from positions of trunks along the first and third PCA axes (PCAbark, PCA_DBH), whose advantage is orthogonality. PCAbark positively expressed the bark cover and negatively decay and contact with soil ($r = 0.85$, -0.93 and -0.62 , respectively; all with $p < 0.001$). PCA_DBH was positively related to the trunk length, DBH and volume ($r = 0.97$, 0.97 and 0.87 , respectively; all with $p < 0.001$). The derived variables were used in results (Fig. 6).

Species composition on trunks. The species occurrence matrix based on data from Electronic Suppl. F, G was studied using gradient analyses in the Canoco ver. 5.12 software (ter Braak & Šmilauer 2012) after deleting rare species occurring only on one trunk (singletons). The total length of the largest distance measured with detrended correspondence analysis (DCA) was 6.38, which allowed us to use the unimodal ordination methods. The relationship between species community pattern and the trunk/habitat variables was tested within a constrained ordination framework (canonical correspondence analysis, CCA) using a Monte Carlo permutation test (MCPT, number of permutations 4999). The explanatory effects of particular environmental variables were evaluated in MCPT with a stepwise procedure of selecting the significant variables, i.e. those having the best fit to species data. As ordinal values of decay stage were not strictly linear, we used the individual decay stages as supplementary nominal variables and projected them passively by the software into separate biplots (as they were insignificant) reflecting the same di-

rections of ordinal space. The difference of the fungal community pattern between ZL and BP was tested using partial CCA with the factor of the host tree. For further explanations, see Šmilauer & Lepš (2014).

Results

Species richness

Zámecký les

We recorded 175 taxa of macrofungi on 18 trunks studied (Electronic Suppl. F, G). They represent 173 species plus 2 varieties of the same species (*Mycena epipterygia*). The high-frequent species are listed in Electronic Suppl. H, I. None of the species was found on all trunks. Most species were basidiomycetes (168 of 175). The species-richest genera were *Mycena* (13 species), *Galerina* (7), *Botryobasidium* (6), *Xylodon* (5), *Hyphoderma* (4), and *Oligoporus* (4). Macroscopic ascomycetes were represented by only 7 species belonging to discomycetes (*Ascochyne cylichnium*, *A. sarcoides*) and pyrenomycetes (*Camarops tubulina*, *Durandiella gallica*, *Echinospaeria canescens*, *Hypocrea citrina*, *H. rufa*). Only *C. tubulina* and *A. cylichnium* were more frequent (5 trunks each).

Picea trunks (12) were inhabited by 142 species with 21–39 species per trunk (Electronic Suppl. F, Tab. 1). The average number of species per trunk

was 30. The most frequent species were *Fomitopsis pinicola*, *Mycena rubromarginata*, *Xylodon asper* and *Physisporinus sanguinolentus*. Almost two thirds of the species (92, i.e. 65 %) were low frequent, found only on one trunk (singletons: 65) and two trunks (doubletons: 27).

Abies trunks (6) were inhabited by 104 species with 23–40 species per trunk (Electronic Suppl. G, Tab. 1). The average number of species per trunk was 32. The most frequent species were *Athelia epipterygia*, *Pluteus pouzarianus* and *Xylodon brevisetus*. Almost three quarters of the species (76, i.e. 73 %) were low frequent, found only on one trunk (singletons: 59) and two trunks (doubletons: 17).

Zámecký les versus Boubínský prales

A total of 307 species were found at both locations (Electronic Suppl. F, G; Tab. 2) on the 66 trunks studied. As shown in Tab. 1 and Fig. 4, no significant difference in fungal richness between individual *Picea* and *Abies* trunks at the same locality was detected, while the effect of locality on a specific tree species was significant (ANOVA F value = 13.4, p = 0.0005). On average, the trunks of both *Picea* and *Abies* were species-richer in ZL than in BP, especially in the case of *Abies*. One outlayer (Fig. 4: at the top right) was the extremely rich *Picea* trunk BB13 (55 species).

Tab. 1. Number of species on *Picea* and *Abies* trunks at Zámecký les and Boubínský prales localities. For simplicity, the two varieties of *Mycena epipterygia* (Electronic Suppl. F, G) are counted as two species.

<i>Picea</i>	Zámecký les (12 trunks)	Boubínský prales (18 trunks)
total no. of species	142	158
no. of species per trunk	21–39	6–55 (mostly 15–40)
<i>Abies</i>	Zámecký les (6 trunks)	Boubínský prales (30 trunks)
total no. of species	104	200
no. of species per trunk	23–40	4–33 (mostly 12–30)
<i>Picea + Abies</i>	Zámecký les (18 trunks)	Boubínský prales (48 trunks)
total no. of species	175	263

Tab. 2. Species occurring on *Picea* and *Abies* trunks at Zámecký les and Boubínský prales localities. For simplicity, the two varieties of *Mycena epipterygia* (Electronic Suppl. F, G) are counted as two species.

	Zámecký les	Zámecký les + Boubínský prales
<i>Picea + Abies</i> , total no. of species	175 (18 trunks)	307 (66 trunks)
<i>Picea + Abies</i> , no. of species occurring on both trees	71 (40.5 %)	130 (42 %)
<i>Picea</i> only, no. of species	71 (40.5 %) (12 trunks)	80 (26 %) (30 trunks)
<i>Abies</i> only, no. of species	33 (19 %) (6 trunks)	97 (32 %) (36 trunks)

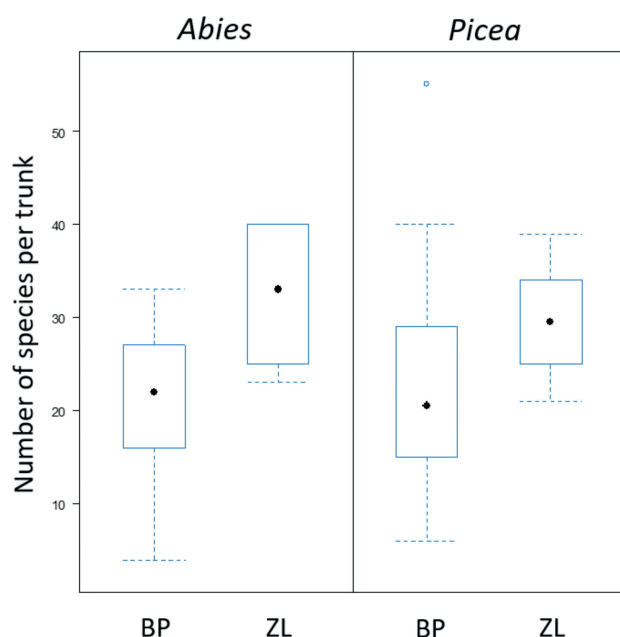


Fig. 4. Range of fungal species richness on all studied trunks in relation to the tree species and locality (BP: Boubínský prales, ZL: Zámecký les). Only the difference between localities was significant (ANOVA F value = 13.4, $p = 0.0005$).

Species composition

Zámecký les

Fungi occurring on both *Picea* and *Abies* trunks represented only 40.5 % of the total species number (Tab. 2). The remaining species were unique to either *Picea* or *Abies* (40.5 %, 19 %; respectively). This shows that the fungal species composition on *Picea* and *Abies* trunks was quite different.

Zámecký les versus Boubínský prales

Combined data for ZL and BP showed a similar percentage of shared *Picea* + *Abies* species (42 %) as

in the ZL itself (see previous section). However, the percentage of species unique to either *Picea* or *Abies* (26 %, 32 %; respectively) was reversed in favor of *Abies* (Tab. 2). This is mainly associated with the big increase of *Abies* species from 30 trunks studied at BP (compare only 6 available trunks at ZL).

If analyzed with multivariate statistical methods (Fig. 5), the species composition of fungal communities on individual trunks was clearly different between ZL and BP, both for *Picea* and *Abies*. Trunks from these two sites formed two separate clusters without any mixing (Fig. 5: right diagrams). Left diagrams of Fig. 5 document again that trunks in ZL are species richer (compare previous section and Fig. 4), a fact even more evident when singletons are eliminated.

The species composition of fungal communities on both *Picea* and *Abies* trunks (Fig. 6: top diagrams) was closely associated with the way of tree fall (uprooted or broken) and two derived variables: PCAbark and PCA_DBH. PCAbark expresses collinear variables bark cover, decay, moss cover, contact with soil and the total canopy cover (see Electronic Suppl. E; note that some of them are correlated negatively, i.e. in opposite direction). PCA_DBH represents the trunk volume parameters (trunk length, DBH, volume). When wood decay stages are passively projected into space defined by these variables, a slightly different trajectory of wood decay for different tree is seen (Fig 6: bottom diagrams) – a curve resembling horizontal letter S for *Picea* and letter U for *Abies*. It shows that the group of species corresponding to the later decay stages 4 and 5 is more distinct in *Abies*, consisting of some mycorrhizal species (*Laccaria amethystina*, *Lactarius subdulcis*) and corticioids (e.g. *Leptosporomyces galzinii*, *Athelia decipiens*, *Hyphoderma cremeoalbum*, *Botryobasidium subcoronatum*).

Tab. 3. Presence of species of special interest (SSI) in Zámecký les and Boubínský prales.

	Zámecký les (12 trunks)	Boubínský prales (18 trunks)
<i>Picea</i> , no. of SSI	30	36
<i>Picea</i> , total no. of SSI from both localities	53	
<i>Picea</i> , no. of SSI common to both localities	13 (25 %)	
	Zámecký les (6 trunks)	Boubínský prales (30 trunks)
<i>Abies</i> , no. of SSI	22	57
<i>Abies</i> , total no. of SSI from both localities	67	
<i>Abies</i> , no. of SSI common to both localities	13 (19 %)	

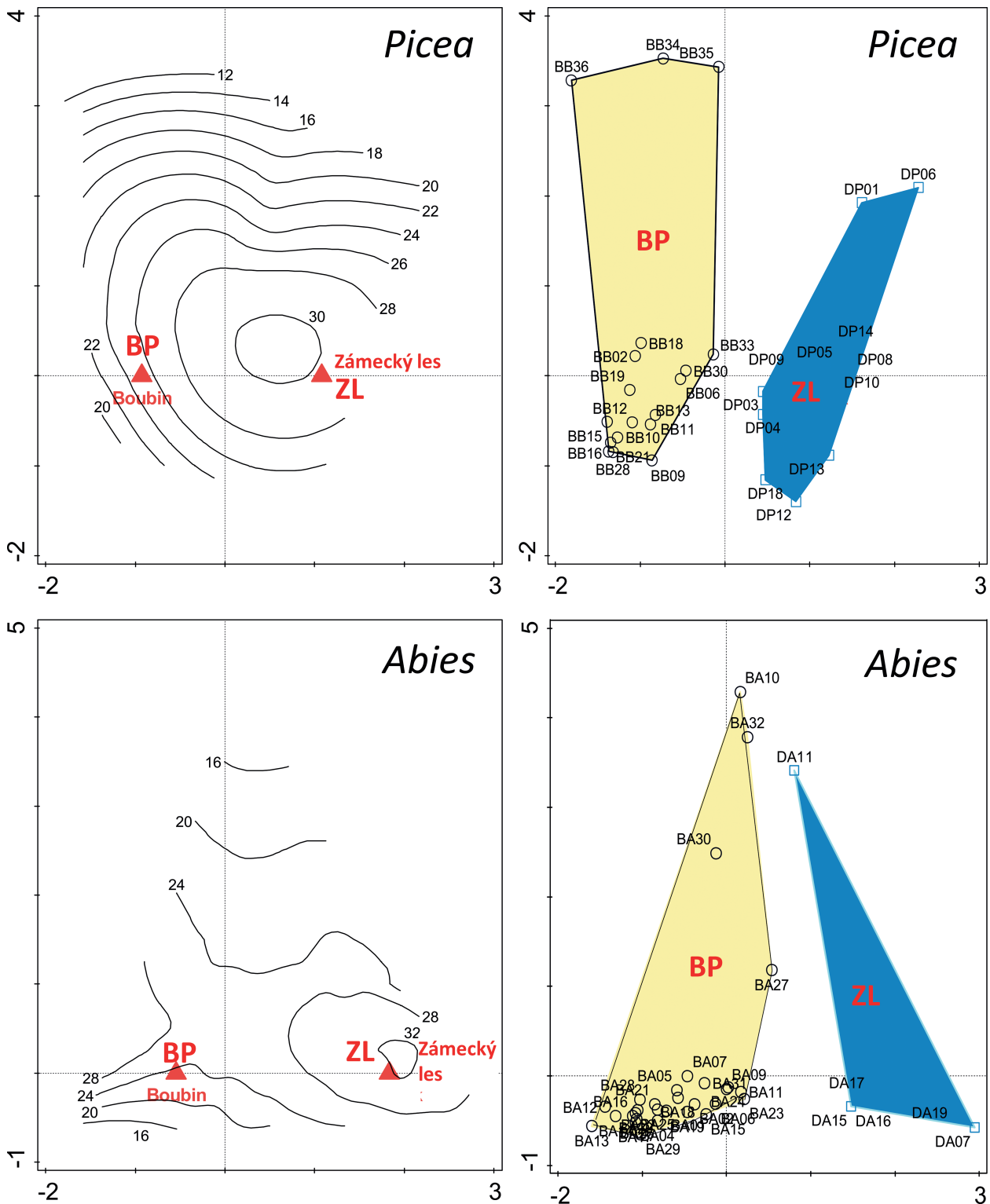


Fig. 5. Ordination biplots (CCA) defined by fungal species patterns for *Picea* and *Abies*. **Left** are isolines showing gradient of fungal richness on trunks at projected localities (BP: Boubínský prales, ZL: Zámecký les). **Right** are centroid positions of fungal communities on the individual studied trunks grouped by locality. For *Picea* and *Abies*, first and second axes explain 18.3 % and 18.8 % of fungal species variation, respectively. For trunk codes (BB, DP, BA, DA), see Electronic Suppl. C, D. Species numbers and community compositions were computed without singletons.

Species of special interest (SSI)

SSI species are less represented in ZL than in BP, both on *Picea* and especially on *Abies* trunks (data: Electronic Suppl. F, G; summarization: Tab. 3). The percentage of SSI species common to both localities (Tab. 3) is relatively low (25 % for *Picea*, 19 % for *Abies*) which means that most SSI are different from one locality to another. When only the most valuable species are highlighted, i.e. the rarest ones and those preferring old-growth forests, the difference between ZL and BP is even greater (Tab. 4). Boubínský prales is much richer in these species, hosting rarities like *Amylocystis lapponica*, *Chrysomphalina grossula*, *Clitocybula familia*, *Cystoderma subvinaceum*, *Dentipratulum bialoviesense*, *Fomitopsis rosea*, *Galerina pruinatipes*, *Ionomidotis irregularis*, *Junghuhnia collabens*, *Kneiffiella altaica*, *K. curvispora*, *Laurilia sulcata*, *Mycena clavata*, *Phellinus pouzarii*, *Pseudoplectanina melaena*, *Resupinatus striatulus* and *Skeletocutis odora* (Tab. 4).

Discussion

Environmental variables shaping fungal richness and species composition on decaying trunks of *Picea* and *Abies* have been thoroughly discussed in our previous papers from BP locality (Holec et al. 2020, 2022a; Holec & Kučera 2020). In agreement with publications cited there, the key role of wood decay stage with associated variables bark and moss cover was shown. Other significant variables are the canopy cover (influencing heat load, amount of precipitation and air humidity), elevation, tree history (expressed by time since death, time since fall and way of fall) and trunk volume. New data from ZL further confirm general importance of these parameters (Electronic Suppl. E, Fig. 6). In the following sections, we will focus on the influence of forest naturalness.

Regarding the relevance of our fruitbodies-based research in the molecular era, we discussed it in detail in previous papers (Holec et al. 2020, Holec & Kučera 2020) showing that this method is not outdated. We agree with the latest synthesis published by Heine et al. (2021). They concluded that eDNA metabarcoding cannot be used interchangeably for morphological community analyses to identify response patterns of fungal communities on forest management strategies. The best way is a combination of both approaches. This is a challenge for future research at our study sites.

Species richness

The fact that the trunks of both *Picea* and especially *Abies* are on average species-richer in forest affected by man (ZL) than in the virgin one (BP) is quite surprising (Fig. 4). We would assume the opposite, especially with regard to the huge species pool and dead wood supply in BP (Holec et al. 2015, Vrška et al. 2012), a site of much larger area (Electronic Suppl. A). It turns out, however, that a certain ecological niche, here a fallen decaying trunk, can be inhabited by a rich community of fungi regardless of the degree of human intervention on the site. It is also likely that the lower elevation of ZL (one of the key factors, see previous section) enables occurrence of higher number of species in comparison with higher-located (= cooler) BP site, especially for *Abies*. The unusual fungal richness of one *Picea* trunk from BP (Fig. 4, Electronic Suppl. F: BB13) is caused by the presence of an extraordinary high number of old-growth forests species that are absent from ZL (Tab. 4).

Most publications simply state that fungal diversity in man-influenced forests is lower than in the natural stands (e.g. Bader et al. 1995, Lindblad 1998, Junninen et al. 2006, Müller et al. 2007, Tomao et al. 2020). However, it concerns the total diversity at study site or plot. Our results show that the discrete substrate units in man-influenced forest may be inhabited by equally rich or even richer fungal communities than in the natural ones. A similar situation was documented by Suominen et al. (2019) based on fruitbodies-based research and Purahong et al. (2014) by molecular methods concluding that „forest management may affect fungal OTU richness in CWD logs in a complex manner“.

However, there is a substantial difference in species composition between trunks in ZL and BP (Fig. 5), which is discussed below.

Species composition

Both in ZL and BP, *Picea* and *Abies* occur together. It would be expected that the dead trunks of these two conifers would host similar fungal communities. However, the difference is quite big. In ZL, the species unique to either *Picea* or *Abies* represent almost 60 % of the total species number and the percentage is almost the same when ZL and BP are counted together (Tab. 2: 58 %). This shows that many species of lignicolous fungi have a relatively strong preference for the tree species they inhabit. This fact was recently stressed e.g. by Rustøen et al. (2023), although in their case the difference especially between deciduous and coniferous trees was

Tab. 4. Comparison of presence of species of special interest (SSI) between Zámecký les (ZL), Mittelsteighütte (MH) and Boubínský prales (BP). Only the rarest and old-growth forest species are shown. See Materials and methods for sources of data, delimitation of SSI species and categories of naturalness, and Electronic Suppl. F, G for presentation of all SSI species.

Locality	Zámecký les (ZL)	Mittelsteighütte (MH)	Boubínský prales (BP)
	Species that are not present in BP and MH (but see explanation for §)	Extra species that are not present in ZL	<i>Normal letters:</i> extra species that are not present in ZL <i>Bold letters:</i> extra species that are not present in both ZL and MH, i.e. unique for BP
Naturalness	near-natural forest	natural forest	virgin forest
SSI species	<i>Cyphella digitalis</i> § A <i>Helicogloea dryina</i> A <i>Hyphoderma obtusifforme</i> § P <i>Kneiffiella floccosa</i> P <i>Oligoporus romellii</i> & P <i>Physisporinus expallescens</i> & A <i>Postia cyanescens</i> & P <i>Trechispora minima</i> & P	<i>Antrodia cretacea</i> (as <i>A. crassa</i>)*** P <i>Arrhenia epichysium</i> *** A, P <i>Chromosera cyanophylla</i> *** A <i>Chrysomphalina grossula</i> *** P <i>Clavulicium macounii</i> ** A, P <i>Clitocybula familia</i> ** A <i>Gyrophanopsis polonensis</i> *** A <i>Kneiffiella curvispora</i> *** A, P <i>Mycena clavata</i> *** A, P <i>Phellinus pouzarii</i> ** A <i>Phlebia cremeoalutacea</i> *** A <i>Pseudoplectania melaena</i> ** A <i>Pseudorhizina sphaerospora</i> *** P	<i>Antrodia cretacea</i> (as <i>A. crassa</i>)* P <i>Antrodia piceata</i> (as <i>A. sitchensis</i>)* P <i>Amylocystis lapponica</i> P <i>Arrhenia epichysium</i> A, P <i>Chromosera cyanophylla</i> * A <i>Chrysomphalina chrysophylla</i> * P <i>Chrysomphalina grossula</i> P <i>Clavulicium macounii</i> A <i>Clitocybula familia</i> A <i>Cystoderma subvinaceum</i> P <i>Dentipratulum bialoviesense</i> P <i>Fomitopsis rosea</i> A, P <i>Galerina pruinatipes</i> A, P <i>Gyrophanopsis polonensis</i> A <i>Hyphoderma involutum</i> P <i>Ionomidotis irregularis</i> A <i>Junghuhnia collabens</i> A, P <i>Kneiffiella altaica</i> A <i>Kneiffiella curvispora</i> A, P <i>Laurilia sulcata</i> P <i>Mycena clavata</i> A <i>Phellinus ferrugineofuscus</i> * P <i>Phellinus pouzarii</i> A <i>Phlebia cremeoalutacea</i> A <i>Pseudoplectania melaena</i> A <i>Pseudorhizina sphaerospora</i> P <i>Resupinatus striatulus</i> P <i>Skeletocutis cummata</i> A <i>Skeletocutis odora</i> A

A on *Abies* trunkP on *Picea* trunk

§ known from Mittelsteighütte according to Nuss (1999) or DGfM (2023)

& recently described, less known species

* species known outside monitored trunks (see Holec et al. 2015)

** according to Nuss (1999)

*** according to DGfM (2023)

shown. Our results document that the difference is distinct even between conifers and at the same site. It is certainly also connected with the different properties of spruce and fir wood, where fir wood is softer, without resin, and therefore rots more easily.

The difference between localities is also high. Fungal communities on trunks in ZL and BP are clearly separated for both *Picea* and *Abies* (Fig. 5). This documents a large influence of factors associated with the locality. As shown in Electronic Sup-

pl. A, the main differing parameters between ZL and BP are the altitude (already discussed above), area and degree of forest naturalness. The last two factors are discussed in the following sections.

Species of special interest (SSI)

This group of species contains not only rare and/or endangered Red List fungi, but also species demonstrably preferring old-growth forests („indicator species“: Bader et al. 1995, Kotiranta & Niemelä

1996, Parmasto 2001, Holec 2003, Christensen et al. 2004, Müller et al. 2007, Blaschke et al. 2009, Dvořák et al. 2017, Halme et al. 2017). SSI species are much less represented in ZL than in BP (Tabs. 3, 4). The most valuable old-growth forest species are totally absent in ZL (see results and Tab. 4; especially *Amylocystis lapponica*, *Phellinus pouzarii*, *Pseudoplectanina melaena*, *Clitocybula familia*), not only from the monitored trunks but also from the whole locality (own data, unpublished). On the other hand, several other valuable species are known from BP outside the studied trunks, namely *Antrodiella cretaea*, *A. piceata*, *Chrysomphalina chrysophylla* and *Phellinus ferrugineofuscus* (Tab. 4). Most of the exclusive ZL fungi (Tab. 4) are represented by recently described inconspicuous species that are likely to be found in BP during a future survey. The Mittelsteighütte reserve is somewhere between ZL and BP (Tab. 4). Generally, the fungal occurrence data from all three sites show a perfect match between representation of SSI species and the degree of forest naturalness: virgin forest for BP, natural forest for MH, and near-natural forest for ZL. It documents that the independent concepts of SSI species (as defined in Materials and methods) and classification of forest naturalness (according to Naturalforests 2023) go well together.

Although ZL belongs to the „worst category“ of natural forests, it still hosts some old-growth forests fungi (Electronic Suppl. F, G). They are less rare than species listed in Tab. 4, but still worth mentioning: *Alutaceodontia alutacea*, *Antrodiella citrinella*, *Baeospora myriadophylla*, *Botryobasidium medium*, *Callistosporium pinicola*, *Camarops tubulina*, *Clitocybula lacerata*, *Crepidotus kubickae*, *Galerina stordalii*, *Gymnopilus bellulus*, *Hericium flagellum*, *Hyphoderma capitatum*, *H. obtusifforme*, *Kneiffiella floccosa*, *K. cineracea*, *Lentinellus castoreus*, *Mycena laevigata*, *Panellus violaceofulvus*, *Phellinus nigrolimitatus*, *Rigidoporus crocatus*, *Steccherinum gracile*. The locality is therefore definitely valuable as regards the wood-inhabiting fungi. The question remains why ZL is not even „better“ when it has a nearby source of mycelia and spores of many other old-growth forest fungi, namely the Mittelsteighütte reserve (Fig. 1c, Tab. 4). It is discussed in the next section.

Naturalness and size, key factors

Based on our data, we agree with Bässler et al. (2010) that silvicultural strategies are very important for preservation of wood-inhabiting fungi in forests, as they influence two key factors responsi-

ble for their diversity: 1) forest naturalness and 2) amount and variety of available resource, i.e. dead wood (Abrego & Salcedo 2013). In general, rich presence of CWD was shown to be essential for high species richness and presence of red-listed species (Juutilainen et al. 2014). The dead wood of large volume proved to be most important (Runnel et al. 2021). Hofmeister et al. (2015) stressed the importance of trunks having diameter >80 cm. All trunks at ZL and BP studied by us were from this size class, however, they differed in fungal richness and composition between the sites. The decisive factor proved to be the degree of naturalness reflecting intensity of past human interventions, especially for the representation of SSI species. The main study site ZL is not just a mere near-natural forest but also a small „island“ (about 8 ha) surrounded by the „sea“ of more or less managed spruce forests. The first phase of selective logging took place already in the 18th century (Electronic Suppl. A). The biggest old trees were cut down, because the current oldest trees are only around 280 years old (compare BP with uninterrupted history, where trees are up to 600 years old, Electronic Suppl. A). The supply of dead wood of old trees was therefore interrupted at ZL, which today is shown in the absence of the most sensitive old-growth forest fungi (Tab. 4).

The importance of the decaying logs continuity was stressed e.g. by Bader et al. (1995) showing that selective logging about 100 years ago significantly decreased both the total species number and the number of threatened species. As documented by Josefsson et al. (2010), just minor forest logging (22–26 cut stumps per hectare) carried out a century ago may have continuing effects on forest characteristics, including dead wood dynamics and the wood-inhabiting fungal community, especially the abundance of red-listed species. Recently, Majdanová et al. (2023) confirmed that forest continuity indicated by the presence of >250 years-old-trees (i.e. those that survived logging and wood extraction around the end of the 18th century, similarly like in ZL site) is crucial for high richness of red-listed species. Our data from BP (Tab. 4) show that only spruces and firs 500–600 years old indicate a true continuity undisturbed by human interventions. Only such trees reach the maximal possible age (for spruce and fir) and then die naturally, providing fungi with the largest possible volume of dead wood. The data from our study and the mentioned papers complement each other nicely. It seems that the most sensitive fungi (those printed in bold in Tab. 4) require completely unbroken continuity and absent from even minimally affected sites.

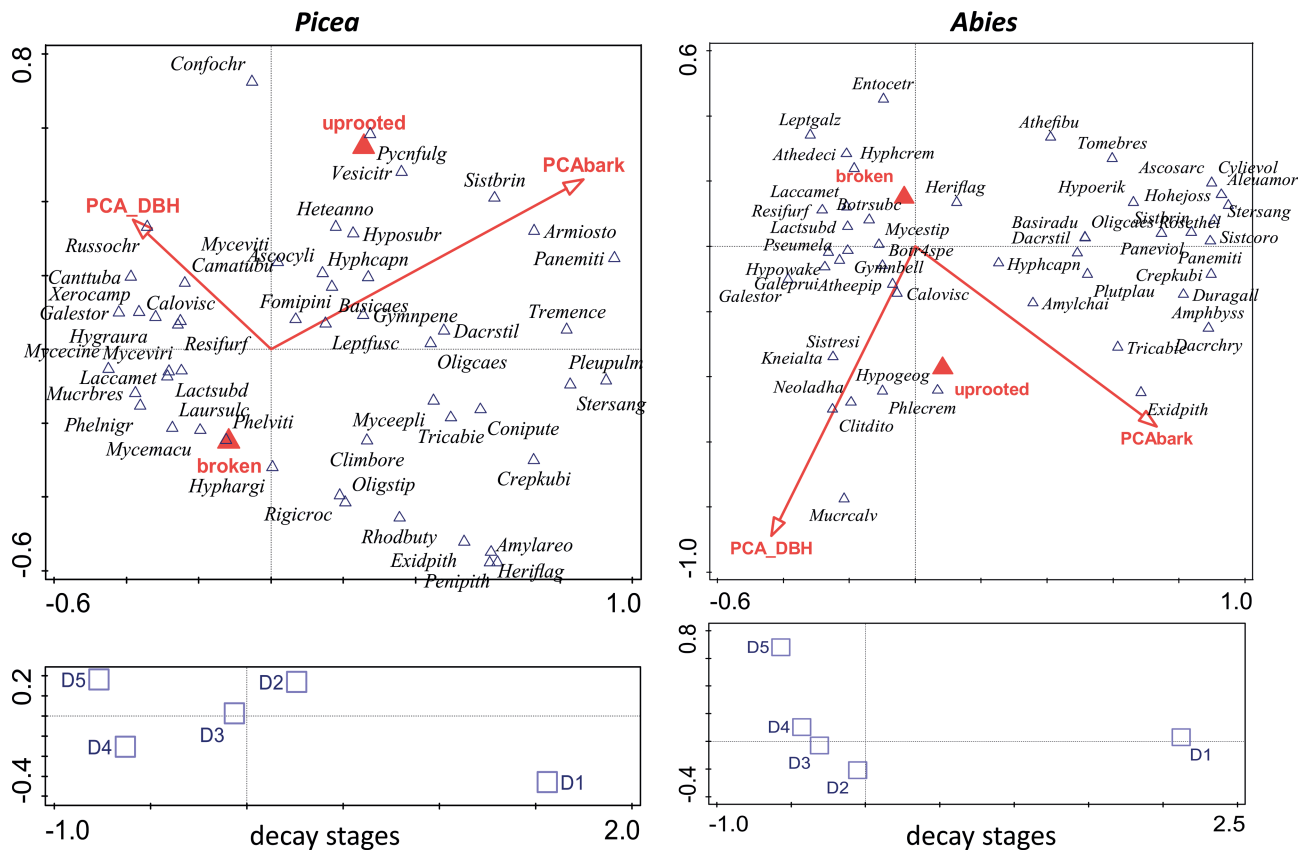


Fig. 6. Ordination biplots (CCA) of fungal species composition on trunks of *Picea* and *Abies* from Zámecký les and Boubínský prales (**top diagrams**). The displayed significant variables (PCA_Bark; PCA_DBH; way of fall with two values: broken, uprooted) explain 17.4 % of total species variance for *Picea* (F-ratio = 1.8, p value < 0.001) and 13.9 % for *Abies* (F-ratio = 1.7, p value < 0.001). The first two axes cover 14.4 % and 11.7 % of cumulative fungal variance, respectively. For full names of the fungi, see Electronic Suppl. F, G. Singletons were excluded from analyses. Only fifty fungal species with higher fit were visualized. In **bottom diagrams**, the categories of decay (D1–D5) are projected passively (see Materials and methods). These diagrams relate to the upper ones and mirror the same quadrants of the biplots.

The small area is another unfavourable factor of the ZL site. The negative effect of forest fragmentation and interrupted connectivity is well known (e.g. Abrego & Salcedo 2014, Abrego et al. 2015, Grilli et al. 2017). Our comparison of ZL and MH, locations situated 3.5 km away, is in line with Abrego et al. (2015) who stressed the importance of connectivity at both site level (= locality area) and the regional scale of 10 km. Even if MH seems to be a perfect pool for recolonization of ZL by rare old-growth forest fungi, the reality is different as the ZL site lacks many valuable old-growth forest species (Tab. 4). Possible causes are discussed in the following section.

Limits to the spread of fungi in old-growth forests

Generally, the pool of available species is very important, being naturally greater in well-preserved and large stands. In them, fungi occurring on

old decaying trunks can gradually colonize newly fallen trunks in their vicinity (Lindblad 1998, Jönsson et al. 2008), that is, over a short distance. Recent studies revealed the dispersal limitation of specialist species already at distances of tens to a few hundred meters from the nearest fruitbody (Norros et al. 2012). It was also shown that most basidiomycete spores fall within 1 m of the cap (Galante et al. 2011), limiting their large-scale dispersal. Our data (especially the comparison of ZL and MH sites in Tab. 4) show that the rare old-growth forest fungi are limited in their ability to spread over several kilometers. On the other hand, the role of wood-inhabiting beetles carrying a broad range of wood-inhabiting fungi and contributing to their dispersal was discovered recently (Seibold et al. 2019, Lunde et al. 2023). All these factors certainly affect the presence/absence of fungi at our sites.

As summarized by Abrego (2022), the ecological assembly processes are regulated by combination of environmental filters (factors preventing or facilitating species colonization and persistence), biotic filters (intra- and interspecific interactions), dispersal (movement and migration) and stochastic processes (random events, especially the priority effects; see e.g. Ottosson et al. 2014, Peay & Bruns 2014). In addition, the role of colonization–extinction dynamics was recently stressed by Moor et al. (2020) who showed that increasing specialization of some species is associated with increasing sensitivity to habitat conditions and increasing extinction rates. On the other hand, the colonization probability increases with larger numbers of suitably large logs in the right decay stage. Thus, forest age and total dead-wood volume are the main variables explaining the colonization probability of wood-decaying fungi (Moor et al. 2020). Interestingly, all species evaluated by Moor et al. (2020) are present in BP, but those of them where the highest degree of specialization has been shown (*Amylocystis lapponica*, *Fomitopsis rosea*, *Phellinus ferrugineofuscus*), are absent in ZL. This is surely connected with the scarcity of suitable substrates in ZL, a small site with partly interrupted continuity (Electronic Suppl. A).

Concluding remarks

Data on the diversity of wood-inhabiting fungi from sites of different naturalness show the importance of linking fungal occurrence data, environmental variables (obtained by field research) and historical data on human interventions in forests (obtained from archival documents, now increasingly available online). The last-named source enables reliable documentation of effects that biologists and ecologists can only capture indirectly or not at all. In our case, the historical data clearly showed the past human interventions, which today are negatively reflected in the representation of rare and old-growth forests fungi. It is a big task for nature conservation in protected areas to minimize the human influence and let the natural processes run, which could support the future return of sensitive species from surrounding refugia, if they still exist.

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Naturalness is key: high species richness of wood-inhabiting fungi does not automatically mean high species quality

Electronic Supplements

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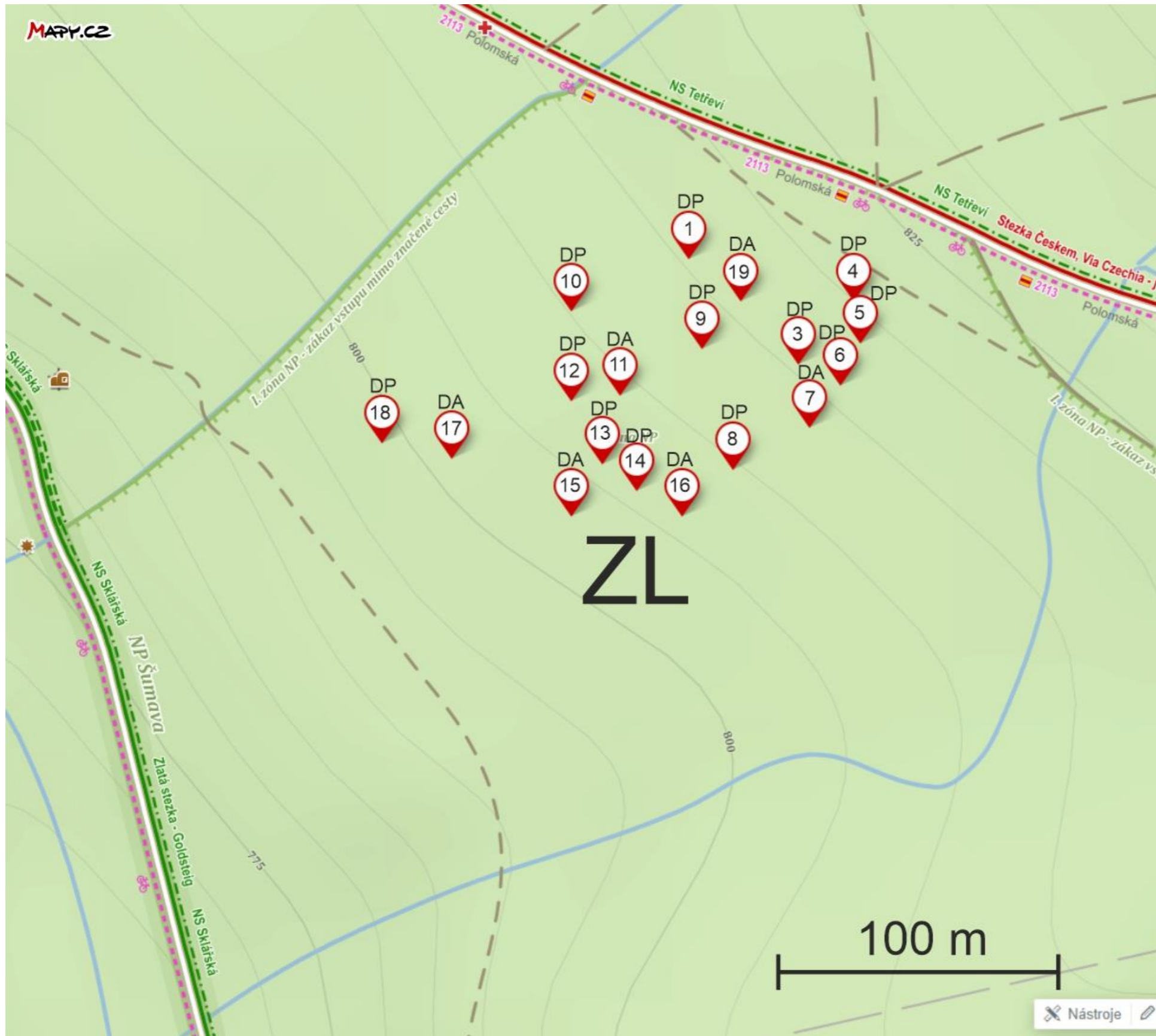
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A. Forest history at Zámecký les (near-natural forest) and localities used for comparison: Boubínský prales (virgin forest) and Mittelsteighütte (natural forest). The colours show the degree of human influence: **green** – almost no human impact, **yellow** – little human impact, **red** – strong human impact. For sources of data see the main paper: Materials and methods, section Study site Zámecký les and the localities compared.

	Zámecký les	Zámecký les - adjacent forest stands	Boubínský prales - core area	Boubínský prales - adjacent forest stands (currently a national nature reserve)	Mittelsteighütte
area (ha)	8	hundreds	47	686	46
elevation (m a.s.l.)	770-825	720-900	925-1120	874-1362	705-810
tree dominants	<i>Fagus sylvatica, Picea abies, Abies alba</i>	<i>Picea abies</i>	<i>Fagus sylvatica, Picea abies, Abies alba</i>	<i>Picea abies, Fagus sylvatica, Abies alba</i>	<i>Fagus sylvatica, Picea abies, Abies alba</i>
period ↓	human interventions ↓	human interventions ↓	human interventions ↓	human interventions ↓	human interventions ↓
1700-1799	probably selective cutting of individual trees (extent unknown)	since 1774: gradual establishment of glass factories in Ferdinandstal (1774) and Deffernik (1786) and the related cutting (extent unknown but old trees left)	no or negligible	no or negligible	no or negligible (1764: construction of Zwieseler Waldhaus)
1800-1880	about 1850-1860: selective cutting (especially of beech) but the forest stand as a whole left as "park forest" (close to Deffernik chateau)	logging for Deffernik glass factories till 1870, about 1855: almost complete deforestation south and east of Zámecký les (see next page), but then continuous forest development: old trees rarely present, juveniles left (both from the original virgin forest)	no or negligible	logging activities at lower elevations and first occasional cutting at Paženi ridge and Mt. Boubín summit; 1870: windstorm and subsequent windfall followed by bark-beetle gradation; large-scale salvage logging (1870-1875) in about half of the territory	selective cutting of individual trees (1850-1914)
1881-1948	forest stand as a whole left as "park forest" (close to Deffernik chateau)	natural reforestation	no or negligible	gradual logging of virgin forest remnants, support of spruce monocultures (removal of beech and fir)	selective cutting of individual trees (1850-1914)
1949-1990	selective cutting of large spruces and firs by Military Forests Enterprise	almost complete deforestation in about 1960, then under ordinary forest management, managed by Military Forests Enterprise	no or negligible	ordinary forest management in younger stands, selective cutting of large trees (both living and dead)	no or negligible
since 1991	rarely selective cutting of spruces attacked by bark beetle, then decorticated and left at site	logging stopped, 1999-2007: cutting of spruces attacked by bark beetle, then decorticated and left at site	no or negligible	occasional logging and the resulting creation of clearings, locally decortication of spruces attacked by bark beetle, wood left at site	no or negligible
partial protection since	± 1779 (construction of Deffernik castle, the forest probably left as adjacent "park")	no	always left untouched (original virgin forest)	part of the territory protected since 1858 within the original virgin forest declared by Count Schwarzenberg: 144 ha + buffer zone	1761-1850: "Bannwald" (economically unused), 1914-1938: "Schongebiet"
strict protection since	1991: natural zone of the Šumava National Park	1995: natural zone of the Šumava National Park	1858: nature reserve declared by Count Schwarzenberg	1958: nature reserve declared by the Czechoslovak Republic	1939: nature reserve, 1997: strictly protected part of the Bavarian Forest National Park
oldest trees *	280	no old trees	500-600	300-580	500
spruce: average age *	150	60-120	ca. 250	80-140	?
fir: average age *	?	60-120	ca. 250	80-140	?
beech: average age *	?	60-120	ca. 250	80-140	?
naturalness	near-natural	man-influenced to man-made	virgin	natural, near-natural, man-influenced	natural

* state in 2020

B. Position and codes of trunks studied in Zámecký les forest (ZL). **DA**: *Abies alba*, **DP**: *Picea abies*. Source of basic map: Mapy.cz (www.mapy.cz), @Seznam.cz, a.s., 2023.



C. Characteristics of Norway spruce (*Picea abies*) trunks studied in **Zámecký les** (coded DP) and **Boubínský prales** (coded BB). More details on trunks in Boubínský prales, e.g. their identification number in database administrated by the The Silva Tarouca Research Institute for Landscape and Ornamental Gardening (RILOG), Brno, Czech Republic, are available in Holec et al. (2020, 2022).

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Trunk code	Latitude coordinate (Northern Hemisphere)	Longitude coordinate (Eastern Hemisphere)	Elevation (m above sea level)	Way of fall	Diameter at breast height [cm]	Length of trunk parts studied, excluding the stump (m)	Volume of lying tree part (m ³); stump not included	Stump	Stump height (m)	Direction of fall (azimuth degrees)	Decay stage	Contact with soil (%)	Bark cover (%)	Moss cover (%)	Cover of trees (%)	Cover of shrubs and young trees (%)	Total canopy cover (%)
Trunk code ↓ Parameter Code →	CoordN	CoordE	Elev	Way_fall	DBH	Length	Vol	Stump	Stump_height	Azimuth	Decay	Soil	Bark	Moss	E3	E2	E32
DP01	N49°07.432'	E13°14.152'	815	broken	120	40,0	15,14	yes	3,5	110	1	100	50	0	70	20	70
DP03	N49°07.412'	E13°14.184'	815	broken	110	44,0	14,00	yes	2,0	60	3	100	30	80	95	0	95
DP04	N49°07.424'	E13°14.200'	820	broken	115	42,0	14,94	yes	1,5	120	3	100	0	90	85	3	85
DP05	N49°07.416'	E13°14.202'	820	uprooted	120	45,0	17,04	no	0,0	50	2	30	20	60	75	10	75
DP06	N49°07.408'	E13°14.196'	815	broken	110	48,0	15,27	yes	1,0	60	1	10	85	0	65	5	65
DP08	N49°07.392'	E13°14.165'	810	broken	95	37,0	8,60	yes	3,0	50	2	35	3	0	70	0	70
DP09	N49°07.415'	E13°14.156'	815	broken	130	44,0	19,54	yes	3,0	10	3	95	0	60	80	0	80
DP10	N49°07.422'	E13°14.118'	810	uprooted	95	47,0	10,93	no	0,0	120	3	40	10	30	65	2	65
DP12	N49°07.405'	E13°14.118'	805	broken	100	39,0	10,26	yes	0,5	45	5	100	0	80	85	2	85
DP13	N49°07.393'	E13°14.127'	805	broken	90	33,0	7,04	yes	1,0	125	4	100	0	90	80	0	80
DP14	N49°07.388'	E13°14.137'	805	uprooted	100	43,0	11,31	no	0,0	90	2	0	10	50	70	5	70
DP18	N49°07.397'	E13°14.063'	800	broken	90	43,5	9,28	yes	0,5	85	4	90	0	80	85	0	85
BB02	N48°58.501'	E13°49.012'	940	broken	100	38,1	12,25	yes	0,0	245	2	5	20	20	30	20	50
BB06	N48°58.451'	E13°48.945'	960	uprooted	100	43,1	12,37	yes	0,0	345	3	50	0	70	30	80	85
BB09	N48°58.401'	E13°48.922'	970	broken	100	17,2	8,55	no	0,0	100	5	100	0	50	5	85	85
BB10	N48°58.396'	E13°48.878'	980	broken	110	36,3	14,62	no	0,0	330	5	98	0	90	60	30	65
BB11	N48°58.369'	E13°48.881'	985	broken	118	46,1	17,16	yes	1,0	90	3	95	50	50	60	60	75
BB12	N48°58.374'	E13°48.743'	1020	broken	110	30,1	13,79	yes	0,5	320	4	90	0	80	40	70	80
BB13	N48°58.411'	E13°48.787'	1010	broken	110	50,3	14,97	yes	1,0	180	3	97	0	50	70	50	80
BB15	N48°58.492'	E13°48.792'	1020	broken	100	41,0	12,36	yes	0,5	220	4	90	0	70	70	50	80
BB16	N48°58.551'	E13°48.705'	1035	uprooted	110	45,1	14,97	no	0,0	85	5	70	0	70	70	30	75
BB18	N48°58.548'	E13°48.879'	980	broken	112	42,4	15,45	yes	2,0	110	3	90	80	70	50	40	65
BB19	N48°58.632'	E13°48.742'	1000	broken	110	38,5	14,78	yes	3,0	180	2	40	60	30	40	50	60
BB21	N48°58.574'	E13°48.893'	970	broken	132	43,5	21,18	yes	1,5	150	4	100	0	80	65	60	75
BB28	N48°58.994'	E13°48.424'	1095	broken	113	39,0	15,60	yes	1,0	165	4	100	0	80	40	50	60
BB30	N48°58.991'	E13°48.453'	1090	uprooted	121	50,5	17,99	yes	0,0	105	2	90	65	60	30	30	35
BB33	N48°58.624'	E13°48.790'	985	uprooted	150	47,6	26,88	no	0,0	90	3	60	70	60	10	30	35
BB34	N48°58.531'	E13°48.913'	965	uprooted	109	50,0	13,61	no	0,0	160	1	20	98	0	30	20	40
BB35	N48°58.510'	E13°48.887'	980	uprooted	135	46,2	22,26	no	0,0	110	1	50	98	0	25	5	25
BB36	N48°58.555'	E13°48.899'	970	uprooted	105	43,5	12,47	no	0,0	115	1	70	100	2	10	5	10

D. Characteristics of silver fir (*Abies alba*) trunks studied in **Zámecký les** (coded DA) and **Boubínský prales** (coded BA). More details on trunks in Boubínský prales, e.g. their identification number in database administrated by the The Silva Tarouca Research Institute for Landscape and Ornamental Gardening (RILOG), Brno, Czech Republic, are available in Holec & Kučera (2020).

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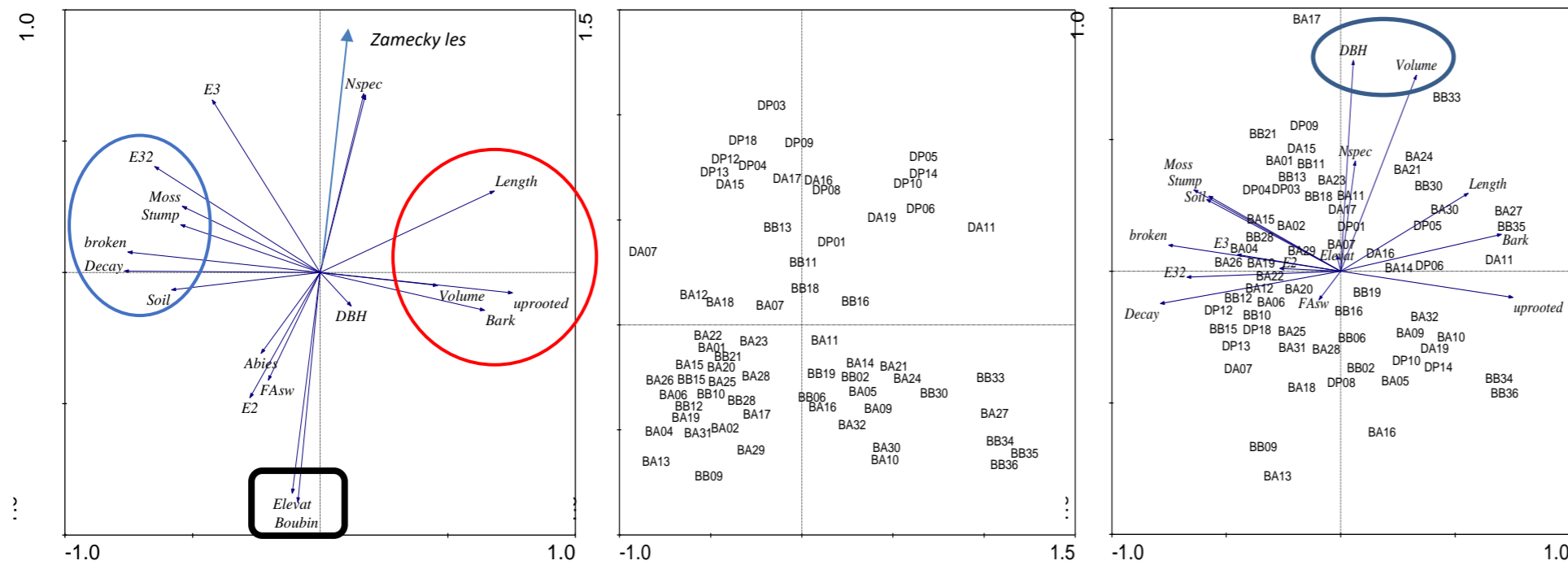
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Trunk code	Latitude coordinate (Northern Hemisphere)	Longitude coordinate (Eastern Hemisphere)	Elevation (m above sea level)	Way of fall	Diameter at breast height [cm]	Length of trunk parts studied, excluding the stump (m)	Volume of lying tree part (m ³); stump not included	Stump	Stump height (m)	Direction of fall (azimuth degrees)	Decay stage	Contact with soil (%)	Bark cover (%)	Moss cover (%)	Cover of trees (%)	Cover of shrubs and young trees (%)	Total canopy cover (%)
Trunk code ↓ Parameter Code →	CoordN	CoordE	Elev	Way_fall	DBH	Length	Vol	Stump	Stump_height	Azimuth	Decay	Soil	Bark	Moss	E3	E2	E32
DA07	N49°07.400'	E13°14.187'	815	broken	90	14,0	5,53	yes	0,0	250	5	100	10	50	85	0	85
DA11	N49°07.406'	E13°14.132'	810	uprooted	105	50,0	14,23	no	0,0	80	1	30	100	2	75	5	75
DA15	N49°07.383'	E13°14.118'	805	broken	115	33,0	11,28	yes	12,0	330	4	100	30	80	75	0	75
DA16	N49°07.383'	E13°14.150'	805	broken	95	41,0	9,54	yes	2,0	100	3	15	70	50	70	5	70
DA17	N49°07.394'	E13°14.083'	800	broken	95	42,0	9,77	yes	3,5	190	2	95	80	50	80	0	80
DA19	N49°07.424'	E13°14.167'	815	uprooted	85	43,5	8,08	no	0,0	85	3	100	50	0	70	20	70
BA01	N48°58.327'	E13°48.750'	1025	broken	130	27,0	14,71	yes	1,0	115	3	80	5	70	70	25	75
BA02	N48°58.369'	E13°48.892'	980	broken	115	26,2	12,60	yes	1,5	220	3	90	15	50	10	90	90
BA04	N48°58.410'	E13°48.862'	990	broken	110	38,0	12,48	yes	1,5	250	5	100	0	60	60	80	90
BA05	N48°58.384'	E13°48.912'	975	uprooted	88	40,8	8,67	no	0,0	200	2	80	95	30	80	50	95
BA06	N48°58.369'	E13°48.943'	970	broken	111	15,3	6,47	yes	6,5	120	4	100	80	50	70	75	80
BA07	N48°58.404'	E13°48.945'	965	broken	111	38,7	8,13	yes	6,0	120	2	60	85	50	75	10	80
BA09	N48°58.450'	E13°48.934'	955	uprooted	100	42,8	10,79	no	0,0	35	3	80	30	40	30	75	80
BA10	N48°58.393'	E13°48.866'	985	broken	96	40,0	10,50	yes	4,0	170	1	25	98	0	20	5	20
BA11	N48°58.442'	E13°48.883'	980	broken	113	33,3	10,83	yes	7,0	100	2	55	90	65	50	50	60
BA12	N48°58.544'	E13°48.885'	975	broken	90	35,2	8,91	yes	1,5	145	3	90	0	80	75	40	85
BA13	N48°58.474'	E13°48.835'	1005	broken	90	13,0	3,42	no	0,0	245	5	100	0	20	75	2	75
BA14	N48°58.463'	E13°48.708'	1045	uprooted	110	43,7	12,59	no	0,0	150	3	90	2	30	70	30	80
BA15	N48°58.473'	E13°48.794'	1015	broken	125	24,6	12,62	yes	2,5	45	5	100	0	40	75	0	75
BA16	N48°58.457'	E13°48.729'	1035	uprooted	85	24,0	7,13	no	0,0	200	3	50	0	30	65	5	65
BA17	N48°58.521'	E13°48.709'	1045	broken	190	17,4	22,28	yes	1,0	145	3	100	10	40	65	20	70
BA18	N48°58.372'	E13°48.931'	970	broken	85	23,7	6,38	yes	2,5	90	3	30	2	50	80	3	80
BA19	N48°58.541'	E13°48.735'	1030	broken	110	27,5	11,51	yes	1,5	125	5	100	0	70	50	30	60
BA20	N48°58.541'	E13°48.703'	1040	broken	96	36,4	9,97	yes	2,5	100	4	100	10	40	60	40	65
BA21	N48°58.558'	E13°48.757'	1015	uprooted	118	47,1	19,56	no	0,0	195	2	80	5	60	60	30	65
BA22	N48°58.559'	E13°48.793'	1010	broken	100	32,1	10,40	yes	1,5	25	3	100	5	60	70	40	80
BA23	N48°58.529'	E13°48.879'	980	broken	127	39,0	10,75	yes	3,5	320	2	80	80	40	80	30	90
BA24	N48°58.320'	E13°48.804'	1010	uprooted	130	42,4	16,08	no	0,0	135	2	80	90	65	60	40	70
BA25	N48°58.638'	E13°48.579'	1045	broken	94	21,4	7,99	yes	11,0	100	4	100	5	60	40	30	50
BA26	N48°58.729'	E13°48.459'	1070	broken	113	26,2	8,47	yes	2,5	200	4	100	0	65	75	20	80
BA27	N48°58.800'	E13°48.469'	1065	uprooted	107	41,6	16,50	no	0,0	115	1	65	100	40	10	10	20
BA28	N48°58.878'	E13°48.518'	1050	broken	100	19,2	8,37	yes	2,0	90	2	20	2	35	60	30	70
BA29	N48°59.000'	E13°48.530'	1090	broken	120	37,0	14,16	yes	0,5	110	4	60	2	25	65	15	70
BA30	N48°59.014'	E13°48.540'	1100	broken	102	44,9	14,86	yes	2,0	160	1	80	98	10	5	15	20
BA31	N48°59.020'	E13°48.516'	1100	broken	100	20,4	8,64	no	0,0	135	3	100	20	40	65	90	90
BA32	N48°58.553'	E13°48.752'	1020	broken	87	42,3	10,94	yes	6,0	135	1	70	98	2	35	15	45

E. Unconstrained ordination biplots (**PCA**) of trunk and habitat variables (**left**) with centroids of trunk positions along the first and second ordinal axes (**middle**), and first and third ordinal axes (**right**). Clumped arrows (highlighted by ellipses) indicate collinear variables. The angles between any two arrows indicate respective pair-wise correlations. Negative correlations are denoted by arrows pointing in opposite directions. For codes of environmental variables see Electronic Supplements C, D. Nspec represents species richness. The folded aspect of fallen trunk to south-west (FAsw) is based on azimuth value and computed as described in Holec et al. (2019).

Reference

Holec J., Běťák J., Dvořák D., Kříž M., Kuchaříková M., Krzyściak-Kosińska R., Kučera T. (2019) Macrofungi on fallen oak trunks in the Białowieża Virgin Forest – ecological role of trunk parameters and surrounding vegetation. *Czech Mycology* 71: 65–89.



F. Fungal species recorded on the studied Norway spruce (*Picea abies*) trunks in Zámecký les (this study, years 2021–2022) and Boubínský prales (data from Holec et al. 2022, year 2020). Cumulated presence/absence data from 4 visits per trunk. Categories of the Czech Red List (Holec et Beran 2006) plus rarity and specificity of some species are indicated in third column (SSI species). For details on trunks (Zámecký les: coded DA, Boubínský prales: coded BA) see Electronic Supplements B, C. Species written in **black occur at both localities, in **red** only in Zámecký les, in **blue** only in Boubínský prales in 2020, in **violet** in Zámecký les and also in Boubínský prales in 2015 (data from Holec et al. 2020).**

Abbreviations:

- * generally rare and old-growth forests species
- ^A as *B. vagum* in Holec & Kučera (2020)
- ^B *Botryobasidium* sp. from 4-species group sensu Bernicchia & Gorjón(2010)
- ^C as *Tulasnella inclusa* in Holec et al. (2022)
- cr: critically endangered
- dd: data deficient
- en: endangered
- nt: near threat
- vu: vulnerable

References

Bernicchia A., Gorjón S.P. (2010) Corticiaceae s.l. – Edizioni Candusso, Alassio.
Holec J., Beran M., eds. (2006): Červený seznam hub (makromycetů) České republiky [Red list of fungi (macromycetes) of the Czech Republic]. – Příroda, Praha, 24: 1–282.
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Holec J., Kučera T. (2020) Richness and composition of macrofungi on large decaying trees in a Central European old-growth forest: a case study on silver fir (*Abies alba*). – Mycological Progress 19: 1429–1443.
Holec J., Kučera T., Běťák J., Hort L. (2020) Macrofungi on large decaying spruce trunks in a Central European old-growth forest: what factors affect their species richness and composition? – Mycological Progress 19: 53–66.

Name ↓ Trunk code →	Name code ↓	Species of special interest (SSI)	Species of special interest (SSI)											Frequency ZL 2021-2022	Frequency BP 2020																			
			DP01	DP03	DP04	DP05	DP06	DP08	DP09	DP10	DP12	DP13	DP14		DP18	BB02	BB06	BB09	BB10	BB11	BB12	BB13	BB15	BB16	BB18	BB19	BB21	BB28	BB30	BB33	BB34	BB35	BB36	
Total number of species on trunk →			21	38	29	34	23	27	34	39	23	28	34	30		26	18	5	13	37	20	52	19	24	32	27	16	19	23	29	13	11	11	
<i>Alutaceodontia alutacea</i>	Alutalut	*								+				1																				0
<i>Ampulloclitocybe clavipes</i>	Ampuclav			+										1																				0
<i>Amylocystis lapponica</i>	Amyllapp	cr												0							+													1
<i>Amylostereum areolatum</i>	Amylareo					+								1												+								1
<i>Amylostereum chailletii</i>	Amylchail											+		1																				0
<i>Amyloenasma grisellum</i>	Amylgris								+					1																				0
<i>Antrodia serialis</i>	Antrseri			+			+							2					+	+	+					+	+	+		+			7	
<i>Antrodia sinuosa</i>	Antrsinu						+							1																				0
<i>Antrodiella citrinella</i>	Antrcitr	en			+								+	2					+															1

Name ↓ Trunk code →	Name code ↓	Species of special interest (SSI)												Frequency ZL 2021-2022														Frequency BP 2020						
		DP01	DP03	DP04	DP05	DP06	DP08	DP09	DP10	DP12	DP13	DP14	DP18	BB02	BB06	BB09	BB10	BB11	BB12	BB13	BB15	BB16	BB18	BB19	BB21	BB28	BB30		BB33	BB34	BB35	BB36		
<i>Xerocomus ferrugineus</i>	Xeroferr												+																				1	0
<i>Xeromphalina campanella</i>	Xerocamp			+																	+		+									1	3	
<i>Xylodon asper</i>	Xyloaspe			+	+	+							+																			8	9	
<i>Xylodon nesporii</i>	Xylonesp												+																			4	0	
<i>Xylodon spathulatus</i>	Xylospat				+								+												+							4	1	
<i>Xylodon brevisetus</i>	Xylobrev			+	+								+																+			6	2	

G. Fungal species recorded on the studied **Silver fir (*Abies alba*)** trunks in Zámecký les (this study, years 2021–2022) and Boubínský prales (data from Holec & Kučera 2020, years 2017–2019). Cumulated presence/absence data from 4 visits per trunk. Categories of the Czech Red List (Holec et Beran 2006) plus rarity and specificity of some species are indicated in third column (SSI species). For details on trunks (Zámecký les: coded DA, Boubínský prales: coded BA) see Electronic Supplements B, C. Species written in **black** occur at both localities, in **red** only in Zámecký les, in **blue** only in Boubínský prales.

Abbreviations:

* generally rare and old-growth forest species

§ species preferring wood of *Abies*

^A as *B. vagum* in Holec & Kučera (2020)

^B *Botryobasidium* sp. from 4-species group sensu Bernicchia & Gorjón(2010)

^C ex aff. *Botryobasidium simile* in Holec & Kučera (2020) = *B. ex aff. conspersum* sensu Zíbarová (2021)

^D as *Tomentella stuposa* in Holec & Kučera (2020)

^E as *Tomentella* sp. sect. *Alytosporium* in Holec & Kučera (2020)

cr: critically endangered

dd: data deficient

en: endangered

nt: near threat

vu: vulnerable

References

Bernicchia A., Gorjón S.P. (2010) Corticiaceae s.l. – Edizioni Candusso, Alassio.

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Name ↓	Trunk code →	Name code ↓	Species of special interest (SSI)	DA07	DA11	DA15	DA16	DA17	DA19	Frequency ZL 2021-2022	BA01	BA02	BA04	BA05	BA06	BA07	BA09	BA10	BA11	BA12	BA13	BA14	BA15	BA16	BA17	BA18	BA19	BA20	BA21	BA22	BA23	BA24	BA25	BA26	BA27	BA28	BA29	BA30	BA31	BA32	Frequency BP 2017-2019			
				23	25	40	33	40	32		22	28	13	22	20	23	19	15	33	28	6	27	12	24	22	19	13	23	31	16	26	30	24	23	32	21	4	26	19	16				
Total number of species on trunk →				23	25	40	33	40	32		22	28	13	22	20	23	19	15	33	28	6	27	12	24	22	19	13	23	31	16	26	30	24	23	32	21	4	26	19	16				
Aleurodiscus amorphus		Aleuamor	§		+					1								+																								3		
Alutaceodontia alutacea		Alutalut	*							0														+																			1	
Amanita fulva		Amanfulv								0															+																			1
Amphinema byssoides		Amphbyss								0																									+								2	
Amylostereum chailletii		Amylchail						+		1						+																			+								5	
Antrodiella citrinella		Antrcitr	en					+		1		+																															1	
Aphanobasidium pseudotsugae		Aphapseu								0		+								+		+												+		+						5		

Name ↓ Trunk code →	Name code ←	Species of special interest (SSI)	DA07	DA11	DA15	DA16	DA17	DA19	Frequency ZL 2021-2022	BA01	BA02	BA04	BA05	BA06	BA07	BA09	BA10	BA11	BA12	BA13	BA14	BA15	BA16	BA17	BA18	BA19	BA20	BA21	BA22	BA23	BA24	BA25	BA26	BA27	BA28	BA29	BA30	BA31	BA32	Frequency BP 2017-2019	
<i>Stereum sanguinolentum</i>	Stersang			+					1								+																				+		+	3	
<i>Stropharia cyanea</i>	Strocyan								0															+																	1
<i>Tomentella bresadolae</i> ^D	Tomebres								0																										+		+		2		
<i>Tomentella microspora</i> s. Svrček 1960 ^E	Tomemicr								0																														+	1	
<i>Tomentella radiosa</i>	Tomeradi								0									+																						1	
<i>Tomentella subclavigera</i>	Tomesubc	*							0																												+		1		
<i>Tomentella sublilacina</i>	Tomesubl						+		1			+						+																						2	
<i>Tomentella terrestris</i>	Tometerr								0																															1	
<i>Trechispora candidissima</i>	Treccand	dd							0		+																													1	
<i>Trechispora hymenocystis</i>	Trechyme								0	+			+														+	+												5	
<i>Trechispora microspora</i>	Trecmicr							+	1																															0	
<i>Tremella encephala</i>	Tremence			+					1																															0	
<i>Trichaptum abietinum</i>	Tricabie			+					1								+																				+			3	
<i>Tricholomopsis decora</i>	Tricdeco								0						+						+						+													5	
<i>Tricholomopsis flammula</i>	Tricflam	*							0	+	+														+			+												5	
<i>Tricholomopsis rutilans</i>	Tricruti								0														+																1		
<i>Tulasnella albida</i>	Tulaalbi						+		1																														0		
<i>Vesiculomyces citrinus</i>	Vesicitr			+	+				2		+						+				+	+							+										8		
<i>Xerocomellus pruinatus</i>	Xeroprui								0	+												+					+													4	
<i>Xylodon asper</i>	Xyloaspe				+	+			2		+		+		+						+					+				+										10	
<i>Xylodon brevisetus</i>	Xylobrev		+		+	+	+	+	5	+																			+	+	+								6		
<i>Xylodon crustosus</i>	Xylocrus		+						1																														0		
<i>Xylodon nespори</i>	Xylonesp		+						1					+														+											2		
<i>Xylodon rimosissimus</i>	Xylorimo								0																											+			1		
<i>Xylodon spathulatus</i>	Xylospat					+			1																+			+		+										3	

H. The most frequent macrofungi on studied trunks of *Picea abies* in Zámecký les (ZL).

The species occur on 6–9 trunks of 12 studied.

Name ↓ Trunk code →	Name code ↓	DP01	DP03	DP04	DP05	DP06	DP08	DP09	DP10	DP12	DP13	DP14	DP18	Frequency ZL 2021-2022
Fomitopsis pinicola	Fomipini		+	+	+		+	+	+	+		+	+	9
Mycena rubromarginata	Mycerubr	+	+	+	+	+	+	+	+			+		9
Physisporinus sanguinolentus	Physsang	+	+	+	+			+			+	+		8
Xylodon asper	Xyloaspe		+	+	+			+	+		+	+	+	8
Botryobasidium isabellinum	Botrisab	+		+	+	+	+	+	+					7
Botryobasidium sp. (from 4-species group sensu Bernicchia et Gorjón 2010)	Botr4spe		+	+	+					+	+	+	+	7
Botryobasidium subcoronatum	Botrsubc		+	+	+		+		+		+	+		7
Dacrymyces stillatus	Dacrstil	+			+	+	+		+			+		6
Gymnopilus penetrans	Gymnpene	+			+	+			+		+	+		6
Hyphodontia pallidula	Hyphpall		+		+		+	+				+	+	6
Hypholoma capnoides	Hyphcapn		+	+	+			+	+			+		6
Lactarius subdulcis	Lactsubd		+	+			+	+		+			+	6
Xylodon brevisetus	Xylobrev			+	+		+	+	+			+		6

I. The most frequent macrofungi on studied trunks of *Abies alba* in Zámecký les (ZL).

The species occur on 4–5 trunks of 6 studied.

Name ↓ Trunk code →	Name code ↓	DA07	DA11	DA15	DA16	DA17	DA19	Frequency ZL 2021-2022
Athelia epiphylla s.l.	Atheepip		+	+	+	+	+	5
Pluteus pouzarianus (incl. P. primus)	Plutpouz	+		+	+	+	+	5
Xylodon brevisetus	Xylobrev	+		+	+	+	+	5
Basidioidendron caesiocinereum s.l.	Basicaes	+		+	+		+	4
Botryobasidium subcoronatum	Botrsubc	+			+	+	+	4
Galerina marginata	Galemarg	+			+	+		4
Ganoderma applanatum	Ganoappl			+	+	+	+	4
Hericium flagellum	Heriflag			+	+	+	+	4
Hypholoma capnoides	Hyphcapn			+	+	+	+	4
Ischnoderma benzoinum	Ischbenz			+	+	+	+	4
Leptosporomyces fuscostratus	Leptfusc		+	+	+		+	4
Mycena purpureofusca	Mycepurp			+	+	+	+	4
Mycena rubromarginata	Mycerubr			+	+	+	+	4
Mycena zephyrus	Mycezeph	+		+		+	+	4