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Comparison of habitats of the rare fungus *Pluteus fenzlii* between Białowieża Virgin Forest (Poland) and thermophilous forests (Slovakia)

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Abstract. *Pluteus fenzlii* is a rare Eurasian lignicolous fungus, an iconic bright yellow species that attracts attention. Its habitat in the Białowieża Virgin Forest, Poland, is dominated by *Carpinus betulus* with admixture of *Quercus robur*, *Tilia cordata* and *Picea abies*, with an herb layer typical for the *Carpinion betuli* alliance. In Slovakia, the country hosting the highest number of localities worldwide, *P. fenzlii* prefers closed canopy of thermophilous forest with dominance of *Quercus cerris* and adjacent *Quercus robur* agg., *Q. petraea* agg., *Carpinus betulus* and *Tilia cordata.* In the Natura 2000 classification this vegetation belongs to habitat 91M0, Pannonian-Balkanic Turkey Oak-Sessile Oak forests, and priority habitat 91G0, Pannonic woods with *Quercus petraea* and *Carpinus betulus*. The Slovak localities can be assigned to the mycosociological community *Boleto (aerei)–Russuletum luteotactae*, typical for thermophilous oak forests of Southern Europe and extrazonal areas in Central Europe. The presence of *P. fenzlii* at the isolated Białowieża locality could represent either a remote site of its present occurrence or a remnant of its former distribution, connected with the relict occurrence of thermophilous vegetation in Białowieża where continental oak forests have already disappeared.

Key words: Central Europe, threatened fungi, habitat, thermophilous vegetation, fungal community, ordination

Introduction

Pluteus fenzlii is a rare Eurasian lignicolous fungus known from only six countries in Europe (Holec et al. 2018). This remarkably yellow annulate species grows on dead wood of broadleaved tree species. It is an iconic species that attracts attention. It usually occurs in hilly areas with more or less natural broadleaved forests, mostly meso- and thermophilous ones, within the transitional zone between hornbeam (alternatively beech) and oak woodlands. However, the species occurs in a wide geographical area and transitional ecological niches in Europe. From west to east, it occurs in foothills of the French Pyrenees in northern basiphilous slope mountain beech forests belonging to the suballiance *Scillo lilio-hyacinthi-Fagenion sylvaticae* and ravine ash forests belonging to the association *Isopyro thalictroidis-Quercetum roboris* from the alliance *Fraxino-Quercion roboris* (Corriol & Moreau 2007). The easternmost European locality is in pine-dominated forests with admixed deciduous trees on carbonate rock covered by loam in the vicinity of the Volga River, Samara region, Russia (Malysheva et al. 2007). The northernmost locality in Central Europe is the Białowieża Virgin Forest in eastern Poland, where *P. fenzlii* grows in hornbeam-dominated deciduous forest of the association *Tilio cordatae-Carpinetum betuli* on glaciofluvial deposits. In the south it is currently reported from Hungary as occurring in acidophilous beech forests of the association *Luzulo-Fagetum* on andesite bedrock and in thermophilous oak forests on sandstone, andesite and alluvial deposits of slightly acidic loess and clay (Holec et al. 2018).

As our previous detailed paper on *P. fenzlii* was focused on its mycological characterization (Holec et al. 2018), the present work describes and discusses in detail the vegetation data of its northernmost isolated locality in Białowieża in a comparison with more diverse localities in Slovakia (the country hosting the highest number of

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its localities worldwide), supplemented with notes on the fungal communities at Slovak sites.

Methods

The vegetation of all known Slovak localities of *P. fenzlii* (for details on their geography see Holec et al. 2018) was sampled by the first author from May 30 to June 1, 2017 (Table 1). The Polish locality was sampled on September 14, 2016 during other study (Holec et al. 2019). All relevés covered the area around fallen trunks with *P. fenzlii*. Sampling covered areas of ~250 m^2. The exact coordinates are not published here, in view of the need for strict nature conservation (protection of rare fungal communities from mushroom pickers), but can be obtained from the authors on request. We sampled the tree (E_3), shrub (E_2) and herb (E_1) layers separately using the Braun-Blanquet phytosociological approach (Kent 2012). Cover-abundance of individual species was estimated on a modified ten-degree Domin-Hadač ordinal scale: r (rare, sterile, seedling), 1 (rare, fertile, few individuals, more seedlings, sapling), 2 (several individuals, cover ~1% of relevé area), 3 (more individuals, cover up to 2%), 4 (more individuals, vegetative dispersed, cover up to 5%), 5 (cover 6–15%), 6 (16–25%), 7 (26–50%), 8 (51–75%), 9 (76–100%). Plant names follow Euro+Med (2006–). Names of syntaxa follow Jarolímek et al. (2008) and Matuszkiewicz et al. (2012).

For comparison of our vegetation relevés with the synthesis of higher units of deciduous forests in Slovakia, we compiled a frequency table (Table 1). Diagnostic, constant and dominant species status and values were taken from Jarolímek & Šibík (2008). Diagnostic taxa are ordered in decreasing value of fidelity (Phi coefficient $\Phi > 0.24$) to display taxa with the best diagnostic capacity ($\Phi > 0.5$, Chytrý et al. 2002). Constant taxa have a percentage frequency of occurrence of more than 25% for classes and more than 40% for alliances, marked "c". Dominant taxa (bolded) have abundance higher than 50% in at least 3% of the relevés.

Unconstrained gradient analysis was computed to visualize the positions of diagnostic species in Canoco 5 (ter Braak & Šmilauer 2012). Individual localities and centroids of higher vegetation units were passively projected to the ordination biplot.

Fungal communities are discussed with respect to Fellner (1984, 1987, 1988) and Šmarda (1972). Lists of fungal species from Slovak localities of *P. fenzlii* were compiled by the second author in collaboration with local amateur mycologists. The Mäsiarsky bok locality was not classified due to insufficient mycological data.

Results

In Białowieża National Park, Poland, one relevé was sampled, as we found *P. fenzlii* at one site only (Table 1, Fig. 1A, B). The canopy was formed by *Carpinus betulus* with additional occurrence of *Quercus robur*, *Tilia cordata* and *Picea abies* in the tree layer. In the shrub undergrowth, only *Carpinus betulus* was rarely present (3%) even though this layer is more represented in the neighbourhood. The herb layer showed average conditions without any significant indication of extreme or different environmental conditions. Species of the herb layer were typical for a higher-level order (alliance *Carpinion betuli* in the Central European concept of the class *Querco-Fagetea*; Fig. 2A, lower left quadrant). Common species of such a hemiboreal forest are typical for both broadleaved and coniferous woods, respectively. At the same site there was a mixture of characteristic species of the alliances *Carpinion betuli* (class *Querco-Fagetea*) and *Piceion excelsae* (class *Vaccinio-Piceetea*): *Oxalis acetosella*, *Gymnocarpium dryopteris*, *Maianthemum bifolium, Dryopteris dilatata, Milium effusum*, *Festuca gigantea* and *Stellaria holostea*. The occurrence of nitrophytes (*Urtica dioica, Geranium robertianum*) and clear-cut species like *Rubus idaeus* shows concurrent human and animal influences on the composition and structure of the forest stand both in the past (coppicing, opening) and at present (overgrazing by wild game, which is currently frequent in Białowieża).

In Slovakia, *Pluteus fenzlii* preferred closed canopy of broadleaved forests (cover 60–80%) with dominance of *Quercus cerris* and *Carpinus betulus*, and adjacent *Quercus robur* agg., *Q. petraea* agg. and *Tilia cordata* (Table 1, Fig. 3). The shrub layer was relatively open (0–25%), with tree layer species and/or meso- xerophilous shrubs forming self-sustaining bushes along the edges (alliance *Prunion spinosae*, class *Rhamno-Prunetea*), such as *Crataegus monogyna*, *C. laevigata*, *Rosa canina* agg. and *Ligustrum vulgare*. Cover of the herb layer varied between 1% and 60%. The average number of herb species per relevé was 24.6. Some characteristic species (dominant and/or frequent) are important indicators. The dominant grasses are typical of broadleaved forests (class *Querco-Fagetea*) and have a wide ecological niche: *Poa nemoralis*, *Brachypodium sylvaticum*, *Dactylis glomerata* subsp. *lobata* and *Melica uniflora*. Similarly, the very frequent forbs *Moehringia trinervia*, *Veronica chamaedrys* and *Geranium robertianum* occur in various forest units. Mesophilous and meso- to eutrophic shade-tolerant hemicryptophytes played an adjacent role in the undergrowth (Fig. 2A, upper left quadrant; *Viola reichenbachiana*, *Fragaria vesca*, *Lamium galeobdolon*, *Pulmonaria officinalis*). The group of diagnostic species of hornbeam, scree and beech woods (*Melica uniflora*, *Galium schultesii*, *Lamium galeobdolon*, *Galium odoratum*, *Mycelis muralis*) was present only on a deep scree slope (Mäsiarsky bok Reserve). Other nitrophilous species like *Urtica dioica*, *Galium aparine*, *Glechoma hederacea*, *Geum urbanum* and *Alliaria petiolata* indicate higher nutrient content and/or anthropogenic impacts, additionally with *Impatiens parviflora*, a neophyte originating from Central Asia.

We were able to distinguish two main types of thermophilous woods inhabited by *P. fenzlii* in Slovakia: (i) oak woods on deeper (basic) substrates with loess, pseudogley or clay soils and species-rich basiphilous vegetation (with *Cornus mas*, *C. sanguinea*, *Ajuga genevensis*, *Lathyrus niger*, *Mellitis mellisophyllum*, *Tanacetum corymbosum*,

Figure 1. *Pluteus fenzlii* basidiomata and habitats. A–B – in Białowieża (photo J. Holec 13.9.2016); C–D – in Slovakia, NNR Boky (photo V. Kunca 15.7.2017 and 24.9.2015); E – Tri chotáre hill (photo T. Kučera 29.5.2017); F – Háj hill (photo T. Kučera 30.5.2017); G – NNR Mäsiarský bok, photo V. Kunca 20.6.2017.

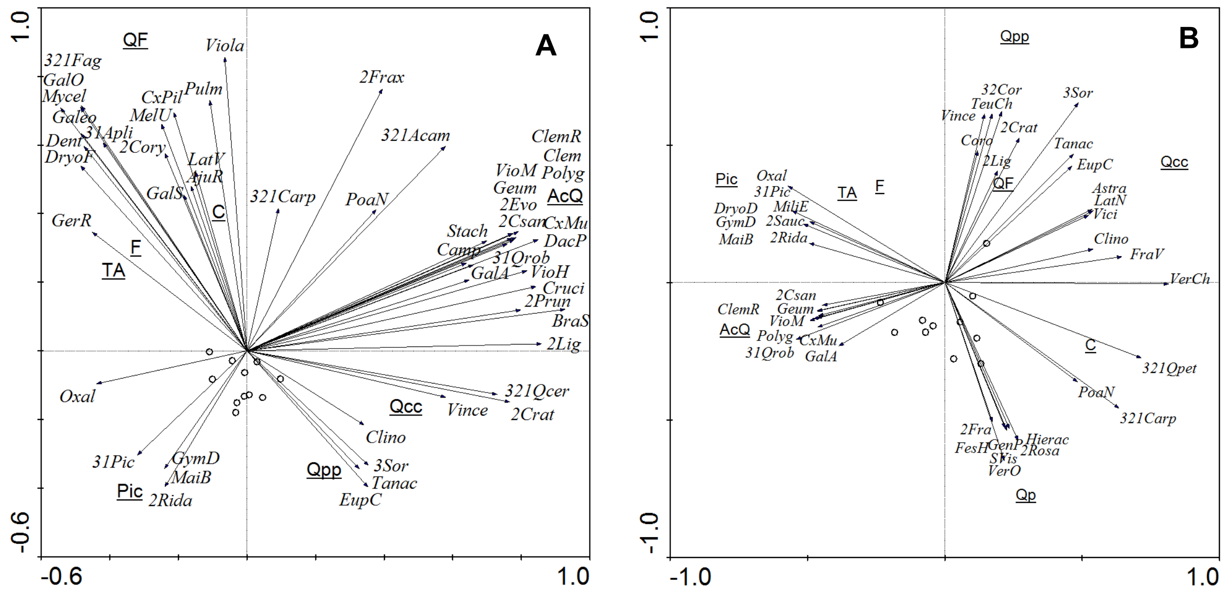

Figure 2. Biplots of principal component analysis (PCA), showing the positions of *P. fenzlii* localities (empty circles) in vegetation space (A – 1st and 2nd axes explain 44% of species variance; B – 3rd and 4th axes 24%). The respective higher vegetation units were taken from the literature (underlined; for full names of vegetation units see explanations in Table 1). For full names of plant species see Table 1. Numbers in front of genera refer to vegetation layer (3 tree, 2 shrub, 1 herb = seedlings).

Vicia cassubica), and (ii) deciduous woods on acidic substrates such as andesite screes, with acidophytes (Fig. 2B, lower right quadrant; *Veronica officinalis*, *Hieracium sabaudum*, *Silene viscaria*). Thermophilous acidophytes occurred on shallow soil on raised andesitic bedrock (*Silene nemoralis*, *Hylotelephium maximum*, *Genista pilosa*, *Campanula persicifolia*, *Verbascum austriacum*; only in Boky Reserve, not visualized).

The presence of hygrophilous species of open habitats, such as *Persicaria hydropiper*, *Carex pallescens*, *Carex remota*, *C. hirta*, *Juncus effusus*, *Lysimachia nummularia* and *Stellaria media*, indicated forest springs and wet depressions (Tri chotáre hill).

Discussion

Poland

Vegetation characterization. The development of the structure and composition of forest communities in Białowieża Virgin Forest differs from that of the rest of Central Europe, due to the lack of *Fagus sylvatica* in the Białowieża region (Faliński 1986). Unlike in Slovakia, we found *Pluteus fenzlii* in shaded linden oak-hornbeam forest (association *Tilio-Carpinetum*) with *Picea abies* admixture (Fig. 1A, B; Holec et al. 2018: Fig. 13). Previous records of *P. fenzlii* in the Białowieża Virgin Forest are not characterized exactly as to the location and vegetation (Gierczyk et al. 2015: forest sections 285B, 284Bd), but most probably originate from a similar habitat (Kwiatkowski 1994). Unlike other areas of hornbeam forest in Central Europe (Ellenberg 1988), the Białowieża forests contain boreal species, ferns and some other species that typically grow in beech forests. In our relevé (Table 1) this is documented by the presence of *Picea abies, Festuca gigantea, Maianthemum bifolium, Oxalis acetosella* and *Trientalis europaea* (the latter outside the relevé) typical for spruce forests, while *Dryopteris dilatata, Galeobdolon luteum, Galium odoratum, Gymnocarpium dryopteris, Hordelymus europaeus* (outside the relevé) and *Milium effusum* represent typical species of suballiance *Eu-Fagenion* (Matuszkiewicz et al. 2012). Very striking is the regular presence of spruce. Unlike the situation in Central European deciduous forests, where spruce is absent in oak forests, in Białowieża it is a very common species, naturally overgrowing lime and hornbeam in the tree layer. The current vegetation is concealed by the expansion of shade-preferring trees like *Carpinus betulus*, documented by a comparative long-term study of permanent plots that began in the 1970s (Kwiatkowska et al. 1997). The most common species of the herb layer currently are *Galeobdolon luteum*, *Stellaria nemorum, S. holostea*, *Galium odoratum*, *Hepatica nobilis*, *Viola reichenbachiana* and *V. riviniana*. The local absence of many meso- and thermophilous species, which are typical for herb-rich hornbeam woods (alliance *Carpinion*) in Central Europe, is very striking (Ellenberg 1988). Thermophilous species are slowly disappearing (*Carlina acaulis*, Łaska 2009), as confirmed by our experience: we have only rarely sampled common thermophilous species such as *Betonica officinalis, Convallaria majalis*, *Daphne mezereum, Lathyrus niger*, *L. linifolius, Lilium martagon*, *Melica nutans* and *Melittis melissophyllum* (Holec et al. 2019).

Holocene history. The background of Holocene history may provide key information to help explain the common occurrence of boreal and thermophilous species in the Białowieża Virgin Forest. It differs from southern parts of Central and Southeastern Europe not only climatically but also by the absence of altitudinal belts in flat relief, yet the vegetation pattern is determined by the heterogeneous mosaic of soil types overlying glaciofluvial sediments up to 800 m deep (Malzahn et al. 2009), which are highly water-permeable and remained frozen relatively long after the retreat of the glaciers (Šafanda et al. 2004; Szewczyk & Nawrocki 2011). This probably allowed numerous postglacial relics as well as boreal and continental species to persist to the present (Kaźmierczakowa & Zarzycki 2001; Adamowski 2009; Pawlaczyk 2009). The tree composition was completed at the turn of the millennium by the expansion of *Carpinus* (Kupryjanowicz 2007; Milecka et al. 2009), supported by past dynamics of fires (Niklasson et al. 2010). The present overgrowth by hornbeam (associated with the falling of the remaining big oak, pine and spruce trees), exacerbated by intensive pasturage or colonization in the past, does not bode well for the future of spruce (and oak). In the long-term perspective, the decline of both oak and spruce threaten the unique mycobiota (Karasiński et al. 2010) of the Białowieża Virgin Forest.

Slovakia

Vegetation characterization. The vegetation maps of temperate forests are very heterogeneous in lower vegetation units along the gradients of altitude, soil, exposure, relief, water and nutrients (Bohn et al. 2004). Slovak localities of *P. fenzlii* (Table 1, 10 relevés; Holec et al. 2018: Fig. 13) are located mostly in the transition between the potential vegetation units of hornbeam woods (suballiance *Carici pilosae-Carpinenion betuli*), xerothermic submediterranean oak woods (alliance *Quercion pubescenti-petraeae*) and/or thermophilous oak woodland (ass. *Quercetum petraeae-cerris*, Fig. 1C–E). One locality (Háj hill near Pravica) represents a transition to subcontinental oak forest (ass. *Potentillo albae-Quercetum*, Fig. 1F). The Mäsiarsky bok Reserve is covered by beech rich submontane forests of suballiance *Eu-Fagenion* (Fig. 1G) (Michalko 1986). In the Natura 2000 classification, all this vegetation belongs to habitat 91M0, Pannonian-Balkanic Turkey Oak-Sessile Oak forests, and priority habitat 91G0*, Pannonic woods with *Quercus petraea* and *Carpinus betulus* (Stanová & Valachovič 2002).

Considerable spatial variation and human impacts probably produced the mixture of plant species of different communities in our relevés, especially at the border of hornbeam and thermophilous oak woods. The spatial pattern of thermophilous oak woodland consists of forest

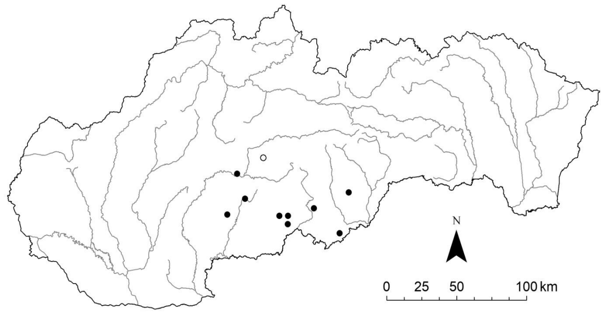

Figure 3. Distribution of *Pluteus fenzlii* localities documented by vegetation relevés (●) in Slovakia, (○) new locality from 2018.

and/or a non-forest habitat mosaic where different mesophilous and thermophilous species merge continuously. For example, *Cornus mas*, *Sorbus torminalis* and *Crataegus monogyna* (Table 1, Háj hill) indicate submediterranean thermophilous oak woods (alliance *Quercion pubescenti-petraeae*), while *Q. cerris*, *Acer campestre* with the forbs *Lathyrus niger*, *Astragalus glycyphyllos* and *Clinopodium vulgare* (Fig. 2B: upper right quadrant) indicate dry mesic oak woods with some acidophilous herbs (alliance *Quercion confertae-cerris,* Jarolímek & Šibík 2008). After finalization of this paper, *P. fenzlii* was found in the Čačínska cerina National Reserve (Fig. 3, empty circle), which is a near-natural forest with predominant occurrence of *Q. cerris*. Several basidiomata were observed by the second author on a fallen decaying trunk of *Q. cerris* on June 1, 2018.

Vegetation classification. Although the classification of oak forests does not seem complicated, it is very difficult to impossible to precisely determine our vegetation relevés and to assign them to associations or higher vegetation units. The number of diagnostic species in our relevés is very low in comparison with vegetation syntheses of thermophilous oak forests of larger areas (Roleček 2005, 2007; Purger et al. 2014). There are two possible explanations for this. (i) Regional vegetation studies contain more characteristic, endangered and rare species, because the widely used preferential sampling of phytosociological relevés is based on the researcher's subjective decision and choice of appropriate relevé plots (Michalcová et al. 2011). Our vegetation sampling, determined by the occurrence of *P. fenzlii*, was closer to a random design of vegetation sampling. Our relevés were sometimes represented by herb-lacking or mixed plots often located in a natural transition of vegetation units or reflecting heterogeneous terrain. As a result, our relevés lack many differential species and in ordination diagram they are positioned in the central part of the biplot (Fig. 2). (ii) In the niche occupied by *P. fenzlii*, average habitat conditions prevail and specialist plant species having higher ecological indicator values are absent. This "biotic filter" exhibits no extraordinary environmental conditions or niche specialization at the level of community structure (van der Maarel 2005; Garnier et al. 2016).

Geographical zonation plays an integral role of dispersal trails in the Hemiboreal (Białowieża), Carpathian, Pontic-Pannonian, subcontinental and submediterranean regions. Southern Slovakia represents the contact zone of the Pontic, Matra and Carpathian biogeographical areas (Bohn et al. 2004). The northern border of the distribution of the Illyrian-Balkan association group is located in southern Slovakia. This vegetation differs from Central European vegetation by its geographically vicariant species (e.g. *Quercus cerris*, *Q. frainetto*, *Fraxinus ornus*, *Castanea sativa*, *Acer tataricum*; Horvat et al. 1974). The numerical classification of Hungarian, Croatian and Serbian oak forests on loess simplified the complicated regional syntaxonomy (consisting of several local associations described in the past; see Borhidi 1996) by delimiting

Table 1. Vegetation relevés.

		Háj hill	Piesok hill 1	hill (315 m) Petrovce	Končitý vrch hill	NNR Boky 1	Tri chotáre hill	Piesok hill 2	NNR Boky 2	Malá obora PA	NNR Māsiarsky bok	Białowieża NP	Querco-Fagetea	Q pub-pet	Q con-cer	Ac tat-Q	Q petr	Carpinion	Tilio-Acerion	Fagion
Cover (%) / Number of relevés																				
E_3 tree layer		80	65	75	85	85	70	80	80	80	60	70								
E_2 Shrub layer		15	15	15	2	5	5	0	15	25	5	3	5669	392	155	42	108	1603	429	2011
E_1 herb layer		60	25	10	1	15	20	5	60	15	60	20								
Trees																				
Cornus mas	E_3	5	.	.	.	.	.	.	3	.	.	.	.	52	.	.	.	.	.	.
	E_2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	E_1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sorbus torminalis agg.	E_3	4	.	.	.	1	.	3	.	.	.	.	.	46	24	.	.	.	.	.
Quercus cerris	E_3	7	7	7	8	7	8	7	7	.	4	.	.	.	**38**	**25**	.	.	.	.
	E_2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	E_1	.	3	1	.	.	3	1	1	.	.	.	.	.	.	.	.	.	.	.
Quercus robur	E_3	.	.	4	3	.	.	.	.	7	3	6	.	.	.	**50**	.	.	.	.
Carpinus betulus	E_3	2	6	7	5	6	5	6	6	5	7	7	**30**	.	25	c	24	**35**	.	.
	E_2	.	5	.	1	3	4	.	4	5	3	3	.	.	.	.	.	.	.	.
	E_1	.	3	.	1	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.
Quercus petraea agg.	E_3	5	.	.	.	5	3	6	.	.	.	.	**c**	.	**24**	.	**29**	**26**	.	.
	E_2	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Acer campestre	E_3	3	3	.	.	.	.	3	4	.	.	.	30	c	25	36	.	25	.	.
	E_2	.	1	3	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
	E_1	.	1	1	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Tilia cordata/platyphyllos	E_3	.	.	.	.	.	.	*3*	.	7	.	4	.	.	.	.	.	.	**33**	.
	E_2	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.
Acer platanoides	E_3	.	.	.	.	.	.	.	.	.	6	.	28	.	.	.	.	.	27	.
	E_1	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.
Fagus sylvatica	E_3	.	.	.	.	.	.	.	.	.	1	.	**35**	.	.	.	.	**c**	**c**	**29**
Picea abies	E_3	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	c
Pinus sylvestris	E_3	.	.	.	.	.	.	*3*	.	.	.	.	.	.	.	.	.	.	.	.
Populus tremula	E_3	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Shrubs																				
Crataegus laevigata/monogyna		3	1	1	1	.	r	.	1	.	.	.	.	28	29	15	.	.	.	.
Ligustrum vulgare		5	1	4	1	.	.	.	4	1	.	.	.	29	30	38	.	c	.	.
Fraxinus ornus/excelsior		r	.	.	.	.	.	.	.	3	1	.	25	.	.	46	.	.	c	.
Evonymus europaea		.	.	1	1	.	.	.	.	1	.	.	.	.	.	33	.	.	.	.
Cornus sanguinea		1	.	.	1	.	.	.	.	.	.	.	.	.	.	24	.	.	.	.
Prunus spinosa		.	.	1	.	.	.	.	1	.	.	.	.	.	c	c	.	.	.	.
Rosa canina agg.		1	1	.	.	1	r	.	1	.	1	.	.	.	.	.	c	.	.	.
Rubus idaeus		1	.	1	.	.	1	*1*	.	.	1	r	.	.	.	.	.	.	.	.
Frangula alnus		.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	c	.	.	.
Herbs																				
Vincetoxicum hirundinaria		.	.	.	.	.	.	.	.	.	r	.	.	27	c	c	.	.	.	.
Teucrium chamaedrys		.	.	.	.	.	.	r	.	.	.	.	.	25	.	.	.	.	.	.
Euphorbia cyparissias		.	1	1	.	.	3	*1*	.	.	.	.	.	c	c	.	.	.	.	.
Tanacetum corymbosum		.	.	.	.	3	r	.	.	.	.	.	.	c	c	.	.	.	.	.
Lathyrus niger		3	1	.	.	.	.	.	.	.	.	.	.	.	34	.	.	.	.	.
Astragalus glycyphyllos		1	.	.	.	.	.	.	2	.	.	.	.	.	29	.	.	.	.	.
Clinopodium vulgare		.	3	1	.	3	.	.	1	.	.	.	.	.	28	.	.	.	.	.
Vicia cassubica		.	r	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.	.	.
Polygonatum latifolium		.	.	.	.	1	.	.	.	1	.	.	.	.	.	50	.	.	.	.
Dactylis glomerata ssp. *lobata*		1	2	1	.	2	.	*1*	.	.	.	.	.	.	c	41	.	c	.	.
Cruciata glabra/laevipes		2	3	.	.	4	1	.	.	.	.	.	.	.	c	33	.	.	.	.
Clematis recta		.	.	1	.	.	.	.	.	.	.	.	.	.	.	30	.	.	.	.
Viola mirabilis		.	.	1	.	.	.	.	.	.	.	.	.	.	.	29	.	.	.	.
Viola cf *hirta*		.	1	.	.	.	.	.	.	.	.	.	.	c	.	28	.	.	.	.
Geum urbanum		*r*	.	1	.	.	.	.	1	r	.	.	.	.	.	27	.	.	.	.
Brachypodium sylvaticum		1	r	2	.	.	.	1	.	.	.	.	.	c	c	25	.	.	.	.
Carex muricata agg.		.	.	1	.	.	1	.	.	.	1	.	.	.	.	25	.	.	.	.
Campanula trachelium/rapunculoides		1	.	.	.	1	.	.	.	.	1	.	.	.	.	c	.	.	.	.
Hieracium sabaudum/racemosum		1	1	.	*r*	1	.	.	.	.	r	.	.	.	.	.	34	.	.	.
Festuca heterophylla		.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	28	.	.	.

Table 1. Continued.

	Háj hill	Piesok hill 1	hill (315 m) Petrovce	Končitý vrch hill	NNR Boky 1	Tri chotáre hill	Piesok hill 2	NNR Boky 2	Malá obora PA	NNR Mäsiarsky bok	Białowieża NP	Querco-Fagetea	Q pub-pet	Q con-cer	Ac tat-Q	Q petr	Carpinion	Tilio-Acerion	Fagion
Pulmonaria officinalis agg.	.	.	1	.	.	.	.	2	1	1	.	34	.	.	c	25	c	c	.
Veronica officinalis	.	1	.	.	1	1	*1*	.	.	1	.	.	.	.	.	c	.	.	.
Genista pilosa	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	c	.	.	.
Carex pilosa	.	.	3	.	.	.	.	.	.	.	.	**32**	.	.	.	.	**42**	.	.
Melica uniflora	3	.	.	.	2	.	.	7	.	3	.	**26**	.	.	.	.	**26**	.	.
Lathyrus vernus	r	.	.	.	.	.	.	.	.	.	.	c	.	.	.	.	25	.	.
Ajuga reptans	1	4	.	.	.	.	.	.	1	.	.	c	.	.	.	.	c	.	.
Galium schultesii	6	.	.	.	1	.	.	.	.	3	.	c	.	.	.	.	c	.	.
Lamium galeobdolon	.	.	.	.	.	.	.	.	.	1	3	27	.	.	.	.	.	27	c
Dentaria bulbifera	4	.	.	*1*	.	.	.	3	1	.	.	31	.	.	.	.	.	25	29
Galium odoratum	5	.	.	.	.	.	.	.	.	2	4	41	.	.	.	.	c	c	28
Viola reichenbachiana	1	.	.	.	.	1	*1*	.	4	.	1	30	.	.	**c**	.	c	.	c
Mycelis muralis	1	r	.	.	.	.	*1*	.	r	1	.	25	.	.	.	.	c	c	c
Dryopteris filix-mas	.	.	.	.	.	.	.	.	.	1	.	c	.	.	.	.	.	c	c
Nitrophilous species	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium robertianum	5	.	.	.	.	.	*1*	3	3	5	1	c	.	.	.	.	.	c	c
Galium aparine	.	.	r	.	.	r	*1*	1	.	1	.	.	.	.	c	.	.	.	.
Urtica dioica	.	.	.	.	.	3	*2*	.	1	5	1	.	.	.	.	.	.	c	.
Alliaria petiolata	.	.	r	.	1	.	.	2	3	.	.	.	.	.	.	.	.	.	.
Moehringia trinervia	.	2	1	.	.	1	1	.	3	1	2	.	.	.	.	.	.	.	.
Fallopia dumetorum	r	1	1	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.
Glechoma hederacea	.	.	.	.	.	3	.	1	1	5	.	.	.	.	.	.	.	.	.
Impatiens parviflora	.	.	.	.	.	.	*2*	4	.	6	.	.	.	.	.	.	.	.	.
Galeopsis speciosa	.	.	.	.	r	.	.	.	1	1	.	.	.	.	.	.	.	.	.
Chelidonium majus	.	.	.	.	.	.	*1*	.	.	2	.	.	.	.	.	.	.	.	.
Other common species																			
Poa nemoralis	1	3	.	.	3	1	*1*	2	.	2	.	c	.	**c**	c	c	**c**	.	.
Veronica chamaedrys	1	3	2	.	2	1	.	1	.	2	.	c	c	c	.	c	c	.	.
Fragaria vesca	r	3	1	.	.	.	*1*	1	.	.	.	c	.	c	.	.	c	.	.
Trifolium medium	1	r	.	.	.	r	*r*	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum	.	1	.	.	1	.	*1*	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria holostea	.	.	.	.	1	.	.	4	.	.	1	.	.	.	.	.	.	.	.

Species present in 1 or 2 relevés: **Háj hill**: *Bromus racemosus* 1, *Convallaria majalis* 1, *Euphorbia amygdaloides* 1, *Lapsana communis* r, *Mellitis melissophyllum* 3, *Quercus petraea* agg. juv. 1, *Ranunculus cassubicus* agg. 1; **Piesok hill 1**: *Allium* sp. r, *Carex* sp. r, *Lathyrus linifolius* (r), *Silene vulgaris* 1, **Piesok hill 2**: *Achillea collina* (r), *Agrimonia eupatorium* 1, *Ajuga genevensis* 1, *Bromus racemosus* 1; **hill (315 m) near Petrovce**: *Ajuga genevensis* 1, *Crataegus monogyna* juv. 1, *Neottia nidus-avis* 1, *Torilis japonica* 1; **Končitý vrch hill:** *Corylus avellana* (1), *Fagus sylvatica* juv. 1, *Neottia nidus-avis* 1, *Tilia cordata* juv. 1; **NNR Boky 1**: *Campanula persicifolia* r, *Fagus sylvatica* juv., r, *Hylotelephium maximum* 1, *Quercus petraea* agg. juv. 1, *Silene nemoralis* 2, *S. vulgaris* 3, *Symphytum tuberosum* 1, *Verbascum austriacum* 1, *Silene* viscaria 1; **NNR Boky 2**: *Cardaminopsis arenosa* r, *Symphytum tuberosum* 3; **Tri chotáre hill**: *Achillea collina* 1, *Carex pallescens* r, *C. remota* r, *C. hirta* r, *Hypericum hirsutum* r, *Juncus effusus* 3, *Lysimachia nummularia* r, *Persicaria hydropiper* 5, *Rubus fruticosus* agg. E_2 2, *Sorbus aucuparia* E_2 1, *Stellaria media* 1; **Malá obora protected area**: *Cardamine impatiens* 1, *Cerasus avium* E_3 3, juv. 3, *Populus tremula* juv. 1; *Quercus robur* juv. 1, *Sambucus nigra* E_2 1, *Stachys sylvatica* 1; **NNR Mäsiarsky bok**: *Allium* sp. 1, *Securigera varia* 2, *Cardamine impatiens* (1), *Epilobium montanum* r, *Fagus sylvatica* E_2 1, *Ribes uva-crispa* E_2 1, *Silene dioica* 1, *Mellitis melissophyllum* (1), *Silene* viscaria 1. **Białowieża NP**: *Dryopteris dilatata* 2, *Festuca gigantea* 2, *Gymnocarpium dryopteris* 4, *Maianthemum bifolium* 3, *Milium effusum* 1, *Oxalis acetosella* 4, *Picea abies* juv. r, *Quercus robur* juv. 1, *Tilia cordata* juv. 1. Plant species presence in the surroundings of relevé (italics) is given here in parentheses.

Explanations

Abbreviations. NNR: national nature reserve, NP: national park, PA: protected area.

Localities in Slovakia. Kremnické vrchy, Zvolen district, near Budča: **NNR Boky 1**, alt. 330 m, steep SSE slope, **NNR Boky 2**, alt. 295 m, steep SE slope. – Krupinská planina, Zvolen district, near Babiná: **NNR Mäsiarsky bok**, alt. 425 m, steep W slope. – Štiavnické vrchy, Krupina district, near Kráľovce-Krnišov: **Končitý vrch hill**, alt. 295 m, gentle NEE slope. – Ostrôžky, Veľký Krtíš district, E of Pravica: **Háj hill** (415 m) alt. 360 m, gentle W slope. – Juhoslovenská kotlina, Lučenec district, near Ľuboreč: **Piesok hill 1**, alt. 245 m, gentle E slope, **Piesok hill 2**, alt. 295 m, steep E slope. – Juhoslovenská kotlina, Poltár district, near Petrovec: **Tri chotáre hill** (276 m), alt. 240 m, gentle N slope. – Juhoslovenská kotlina, Rimavská Sobota district, near Teplý Vrch: **Malá obora** protected area, alt. 230 m, gentle NE slope. – Cerová vrchovina, Rimavská Sobota district, near Petrovce: **hill (315 m)** between **Petrovce** and Jestice villages: alt. 290 m, gentle S slope. For details see Holec et al. (2018).

Locality in Poland. Podlasie Province, Hajnówka district, **Białowieża NP**: alt. 150 m, flat terrain. For details see Holec et al. (2018).

Syntaxa names in column heads (bolded, see below) and abbreviations (in parentheses) are followed by the number of processed relevés: cl. ***QUERCO-FAGETEA*** Br.-Bl. et Vlieger in Vlieger 1937 (QF), subcl. *Fagetalia* Pawłowski in Pawłowski et al. 1928: all. ***Carpinion*** *betuli* Issler 1931 (C), all. ***Tilio-Acerion*** Klika 1955 (TA), all. ***Fagion*** *sylvaticae* Luquet 1926 (F); subcl. *Quercetalia pubescenti-petraeae* Klika 1933: all. ***Q****uercion* ***pub****escenti-****pet****raeae* Br.-Bl. 1932 (Qpp), all. ***Q****uercion* ***petr****aeae* Zólyomi et Jakucs ex Jakucs 1960 (Qp), all. ***Ac****eri* ***tat****arici-****Q****uercion* Zólyomi et Jakucs 1957 (AcQ), all. ***Q****uercion* ***con****fertae*-****cer****ris* Horvat 1954 (*~*petraeae*) (Qcc), cl. *Vaccinio-Piceetea* Br.-Bl. in Br.Bl. et al. 1939, all. *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 (Pic). Dominant taxa (bolded) have abundance higher than 50% in at least 3% of the relevés six communities of wider rank (Purger et al. 2014). The southern Hungarian localities of *P. fenzlii* belong to the submediterranean *Ruscus aculeatus* type, similarly as in the *P. fenzlii* type area (Holec et al. 2018) in the Fruška Gora Hills, Serbia (Fig. 1B in Purger et al. 2014).

Fungal communities. Fungi and their communities are more or less dependent on plants but they are necessary for the existence of most phytocoenoses and also affect their composition (Winterhoff 1992), being symbionts of most plants (parasites, mycorrhizal partners, endophytes) and decomposers of their biomass. Most fungal communities tend to be closely connected with certain plant communities.

Fungal communities of thermophilous oak forests in Central Europe are very specific (Fellner 1984). From the mycocoenological point of view, all evaluated localities of *P. fenzlii* in Slovakia can be assigned to the community *Boleto (aerei)–Russuletum luteotactae* (Šmarda 1972; Fellner 1988). This is typical for the thermophilous oak forests of Southern Europe and rarely present in extrazonal sites in the Central Europe (Bujakiewicz 1992). At all evaluated localities, *Boletus aereus* was present, being a distinctive species of the aforementioned community (Šmarda 1972). Some of the other characteristic fungal species occurring at almost all evaluated localities of *P. fenzlii* are *Amanita caesarea, Aureoboletus gentilis, Boletus moravicus, B. rhodoxanthus* and *Leccinum crocipodium* (see Methods for data). We consider the co-occurring species *Boletus appendiculatus, B. impolitus, B. regius* and *Omphalotus olearius* to be further subcharacteristic species of this fungal community.

In general, knowledge of the species richness and distribution of fungi in Slovakia is deficient, far from complete, and varying strongly among regions (Adamčík et al. 2003). There are only a few works on the mycobiota of oak-dominated forests in Slovakia (Mihál 1995; Mihál 2006; Pavlík & Pavlíková 2006; Ripková et al. 2007). The fungal community at Končitý vrch hill has been classified as *Boleto* (*aerei*)*–Russuletum luteotactae* (Kunca 2012). However, no fungal lists are available for many localities important to nature conservation. Such is the case of the Boky National Nature Reserve (NNR), one of the best-preserved old-growth oak forests, which is under almost no human impacts (Saniga et al. 2014). Only some species and records on dead wood were published from this locality (Vlasák 1989; Kotlaba 1997). Mihál (pers. comm.) recorded *Boletus aereus*, *B. appendiculatus, B. rhodoxanthus* and *B. impolitus* there, which shows that the local fungal community is of a similar character to other Slovak sites of *P. fenzlii*. For Mäsiarsky bok National Nature Reserve, where no relevant data were available for our research, only three *Lactarius* species have been published (Caboň and Adamčík 2014). This locality was visited by the second author only twice. Some interesting lignicolous species were found (e.g. *Buglossoporus quercinus, Ceriporiopsis gilvescens, Hericium cirrhatum*, *Phellinus contiguus*), and no specific ectomycorrhizal ones. The reason for their low occurrence could be the rocky and scree terrain in this reserve.

Concluding remarks

In the Białowieża Virgin Forest, fungi typical for boreal old-growth coniferous forest (*Amylocystis lapponica*, *Phellinus nigrolimitatus, Phellinidium ferrugineofuscum*, Alfredsen et al. 2014; Karasiński & Wołkowycki 2015) encounter species preferring thermophilous oak forests, at least in Europe (e.g. *Hapalopilus croceus*, Fraiture & Otto 2015; *Spongipellis litschaueri, Grifola frondosa,* Karasiński & Wołkowycki 2015). Thus, the find of *Pluteus fenzlii* could represent either a remote site of its present occurrence or a remnant of its former distribution. Its occurrence at an isolated locality could be a consequence of global warming (Andrew et al. 2016). A similar case was documented for recent records of the Mediterranean fungus *Gymnopilus suberis* in the region of thermophilous vegetation in the Czech Republic (Holec et al. 2016). On the other hand, *Pluteus fenzlii* might be considered a relict of retreating continental oak forest in the Białowieża Virgin Forest. Continental oak woods were well represented in the past in Białowieża (Faliński 1986). In terms of site requirements they were similar to current stands of open thermophilous oak woods in southern Slovakia, where 11 localities of *P. fenzlii* are known at present (Holec et al. 2018; this paper).

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