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Old-growth forest fungi – new localities and habitat and host preferences in Slovakia (I)

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"Old-growth forests" comprise habitats from untouched, primeval forests to partially man-influenced, near-natural forests. Some fungal species occur preferably in these forests with a high degree of naturalness. Occurrence data from Slovakia for five wood-inhabiting fungal species was processed. The numbers of known localities of these species in Slovakia range from 4 to 49. The five species prefer different stages of wood decay when producing fruitbodies.

Records of the studied species indicate that *Amylocystis lapponica* and *Ionomidotis irregularis* occur only in old-growth forests, especially in the best-preserved virgin and natural ones, in Slovakia typically on wood of only one or two tree species. *Antrodia labyrinthica* occurs in natural and near-natural forests, while the remaining two species can survive in managed forests with a natural tree composition, localised close to forests of higher naturalness (*Skeletocutis odora*) or even in more intensively managed forests with a small amount of decaying wood and parks (*Yuchengia narymica*). The substantial increase in the number of records of some species in Slovakia can be related to more intensive research in montane old-growth forests (e.g. *Amylocystis lapponica*) or probably to a massive spread of species (*Yuchengia narymica*), even in a wide elevation range.

Key words: *Amylocystis lapponica*, *Antrodia labyrinthica*, *Ionomidotis irregularis*, *Skeletocutis odora*, *Yuchengia narymica*, decay stage, forest naturalness.

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Pralesy a prírodné lesy zahŕňajú biotopy od nedotknutých pralesov až po čiastočne človekom ovplyvnené, prírode blízke lesy. Niektoré druhy húb sa vyskytujú prednostne v týchto lesoch s vyšším stupňom prirodzenosti. Spracovali sme údaje o výskyte zo Slovenska pre päť drevných druhov húb. Počty známych lokalít týchto druhov sa na Slovensku pohybujú od 4 do 49. Týchto päť druhov húb pri produkcii plodníc špecificky preferuje rôzne štádiá rozkladu dreva.

Nálezy hodnotených druhov na Slovensku naznačujú, že *Amylocystis lapponica* a *Ionomidotis irregularis* sa vyskytujú iba v najlepšie zachovaných pralesoch a prírodných lesoch, typicky na dreve iba jedného alebo dvoch druhov drevín. *Antrodia labyrinthica* sa vyskytuje v prírodných a prírode blízkych lesoch, zatiaľ čo ďalšie dva druhy môžu prežiť v obhospodarovaných lesoch s prirodzeným drevinovým zložením, ktoré sú v blízkosti lesov s vyšším stupňom prirodzenosti (*Skeletocutis odora*) alebo niektoré dokonca aj v intenzívnejšie obhospodarovaných lesoch s malým množstvom rozkladajúceho sa dreva a v parkoch (*Yuchengia narymica*). Podstatný nárast počtu záznamov niektorých druhov na Slovensku môže súvisieť s intenzívnejším výskumom v horských pralesoch a prírodných lesoch (napr. *Amylocystis lapponica*) alebo pravdepodobne s výrazným šírením druhov (*Yuchengia narymica*), dokonca v širokom výškovom rozpätí.

INTRODUCTION

Mycological research in old-growth forests in Slovakia has a long historical tradition, especially thanks to Czech mycologists. Its results can be found in e.g. Kotlaba et Pouzar (1962, 1963), Kotlaba (1984), Vlasák (1989), Vampola et Pouzar (1993), Kuthan et al. (1999) and Antonín et al. (2011). However, recent regular mycological research in old-growth forests in Slovakia has hardly been conducted. Sporadic mycological activities and complex results have lately only been published in Adamčík et al. (2007, 2016), Bučinová et al. (2012), Kunca (2016), Ujházy et al. (2018) and Tejklová et Zíbarová (2020). However, some systematic mycological research in these forests is in progress at selected localities and is aimed at fallen trunks of *Abies alba* (Kunca, in prep.) or deals with complex mycofloristic research of old-growth forests in the Liptov region (Peiger et Tomka, in prep.).

Especially wood-inhabiting fungal species are confronted with the current anthropogenic threats like deforestation, loss of old-growth forests, logging, silvicultural intensification and clear-felling (Fraiture et Otto 2015). Many threatened wood-inhabiting fungi are dispersal-limited and depend on landscape-level connectivity to retain viable populations (Abrego et al. 2016). In Slovakia, old-growth forests and their remnants cover 0.47% of the total forested area, which is 0.21% of the country's land area (Jasík et al. 2017, Mikoláš et al. 2019). They are distributed unequally across the country, especially caused by landscape morphology and fragmented and threatened by human activity (Mikoláš et al. 2019).

Around 1500 fungal species grow on dead or dying wood in Central European forests (Leuschner et Ellenberg 2017). Occurrence and survival of some of these species are more or less strictly limited to ecosystems with no or a negligible current and historical influence by man coupled with timber removal (Adamčík et al. 2016, Horák et al. 2016, Dvořák et al. 2017, Purhonen et al. 2021). There are thus substantial differences in the presence of various fungal species between managed and old-growth forests (Bässler et al. 2012, Pouska et al. 2017, Krah et al. 2018), especially in the case of polypores (Penttilä et al. 2004, Berglund et al.

2011, Nordén et al. 2013). Wood-inhabiting fungi are good indicators of environment quality and are often used to evaluate the nature conservation value of forests. They can be used not just as fungal diversity surrogates, but generally as biodiversity surrogates (Adamčík et al. 2007, Hofmeister et al. 2015, Halme et al. 2017). Especially polypores can serve as a flagship group to indicate changes in biodiversity (Holec et al. 2019, Jaroszewicz et al. 2021, Runnel et al. 2021), as some of these species reflect the long-term presence of deadwood and naturalness of forest ecosystems (Alfredsen et al. 2014, Holec et Kučera 2020, Holec et al. 2020). However, some of these rare species can even occur in semi-natural forests in urban areas (Korhonen et al. 2021).

Some wood-inhabiting fungal species are very rare or threatened. In Slovakia, *Amylocystis lapponica*, *Skeletocutis odora* and *Yuchengia narymica* (as *Perenniporia narymica*) are red-listed (Lizoň 2001) but only *A. lapponica* is legally protected (Peiger 2021). Dahlberg et Croneborg (2003) included *A. lapponica* and *S. odora* among 33 threatened fungi in Europe. Three of the studied species are discussed and evaluated in The IUCN Global Fungal Red List: *Amylocystis lapponica* as a least concern species (LC; Dahlberg et Ainsworth 2019), *Ionomidotis irregularis* (preliminarily assessed as vulnerable) and *Skeletocutis odora* (still under assessment).

In our research, new localities of and data on several rare wood-inhabiting fungal species have been recorded and some relationships with naturalness of localities and stage of wood decay in these species records have been observed. Comparing historical records, general trends in the occurrence of the studied species are outlined. This paper is the first contribution of a series in which the different ecological and habitat aspects of these fungi which occur mostly in well-preserved forests in Slovakia will be presented and discussed.

MATERIAL AND METHODS

We compiled a database of records and collections of five lignicolous species in Slovakia by processing the authors' personal records [private fungaria of Vladimír Kunca (PVKU), Maroš Peiger (PGRMRS) and Pavol Tomka (TMKPVL)], temporal personal fungaria of Jan Běťák and Daniel Dvořák (specimens will be deposited in BRNU), data from public fungaria [BRA, BRNM, BRNU, MJ, PRM, PRC, SLO – abbreviations of public herbaria according to Index Herbariorum (Thiers on-line)], the private fungarium of Josef Vlasák (JV; Vlasák on-line) and published documents.

Classification of forest stands in terms of management and naturalness follows Holec et al. (2015a). Old-growth forests are classified as virgin forests (almost unaffected by humans, typical by natural tree species composition, spontaneous development, multi-aged structure, long continuity and the fact that they have never been completely felled), natural forests (formed by natural processes but influenced by human activities in the past – 50 or more years ago) and near-natural forests (tree species composition largely corresponding to habitat conditions but with a simpler spatial structure than in virgin or natural forests, having been formed by human impact, traces of

which are still present). Other forests were generally classified as managed (man-influenced forests). A special category applied here for one species was parks. None of the studied records was found in man-made forests (plantations having a completely unnatural tree species composition). The degree of naturalness was taken from an unpublished map related to the work by Jasík et al. (2017). Some localities were characterised as transitional between these categories, because some of their parts differ in the historical influence by man. These differences in 'quality' were observed at localities in the field or are distinguished as different segments of a locality depicted in the above-mentioned map. Not all localities, especially those related to some historical records, could be valued for their forest naturalness. We also considered the enlistment of the studied localities in the list of old-growth forests (defined as min. 20 ha in area) and their remnants (defined as min. 5 ha in an area of up to 20 ha) in Slovakia (www.pralesy.sk/lokality/). Smaller (less than 5 ha) well-preserved areas were defined as 'fragments'.

The estimation of decay stages followed Heilmann-Clausen (2001): (1) trunks covered with bark without visible signs of decay, (2) decay signs indistinct, wood and bark weakly disrupted, (3) wood decay distinct, bark partially loosening or cracking, (4) wood strongly damaged, soft, but still with a visible structure, in the major part without bark, (5) rotten to almost humified trunks.

Abbreviations used in this paper: NNR – National Nature Reserve, SOD – stage of decay.

RESULTS AND DISCUSSION

The compiled data records of the studied species are listed in the Electronic Supplement. Tab. 1 presents summarised data on the degree of forest naturalness of the localities with occurrence of one or more of the five studied wood-inhabiting fungal species in Slovakia discussed further.

Tab. 1. Studied fungal species and degree of forest naturalness at localities of their occurrence in Slovakia.

Species	Virgin	Virgin to natural	Natural	Natural to near-natural	Near-natural	Near-natural to managed	Managed	Park	Localities total*
Amylocystis lapponica	5	2	4	2					13
Antrodia labyrinthica		2	2	2	2				8
Ionomidotis irregularis	2			2					4
Skeletocutis odora	4	5	2	9	4	3	3		30
Yuchengia narymica	4	3	3	7	5	5	19	2	48

* Not all localities could be valued for their forest naturalness, therefore two localities of *Skeletocutis odora* and one of *Yuchengia narymica* are not included in this table.

Amylocystis lapponica

To date altogether 13 localities of the species (Fig. 1) are known in Slovakia (Fig. 2). It prefers montane old-growth forests here, mainly virgin and natural ones (Tab. 1). These forests consist of a mixture of spruce, fir and beech or

Fig. 1. *Amylocystis lapponica*, Veľká Fatra Mts., Škribňovo near-natural to natural montane forest, wood of *Picea abies*, 3 Nov. 2018 (TMKPVL, MJ 5805). Photo M. Peiger.

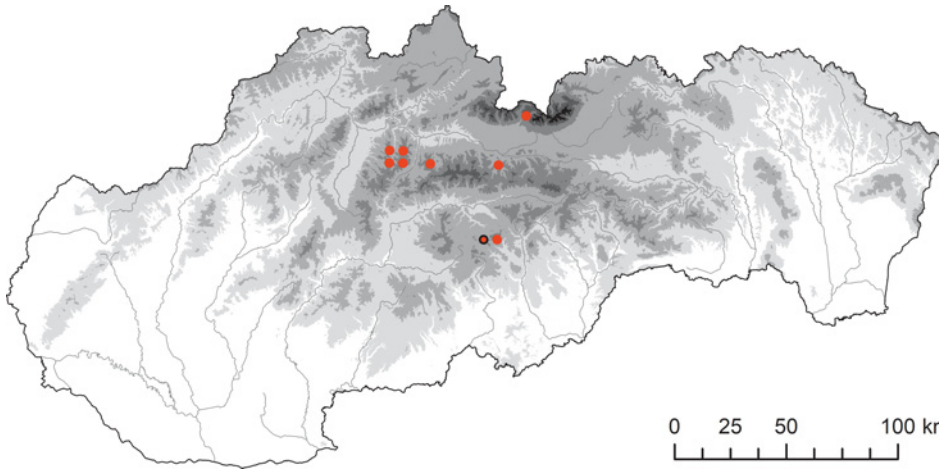

Fig. 2. Distribution of *Amylocystis lapponica* in Slovakia (13 localities). One dot may represent several closely situated localities. Shaded areas indicate altitudinal zones (up to 300 m, 300–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m and over 2000 m a.s.l. – the darker the area, the higher the elevation). Black dots represent historical records until 2000, red dots recent records since 2001, black-red dots a combination of historical and recent records in the same area.

spruce only. Fruitbodies were observed at approx. 700 to 1500 m a.s.l., at the end of summer and in autumn. New localities and records were found on 31 fallen trunks exclusively of spruce in late initial and intermediate stages of wood decay (predominantly SOD 3).

Kotiranta et Niemelä (1993) proposed *Amylocystis lapponica* as an indicator of biotic integrity and conservation value for coniferous boreal virgin forests and the species is often used as an indicator of old-growth forests, for assessing the conservation value of habitats (Bredesen et al. 1997) or as a test species in different habitat modelling and evaluations (Siitonen et al. 2005, Berglund et al. 2011, Mair et al. 2018, Nordén et al. 2018, Moor et al. 2021). It has also been used to study the recovery of a fungal species population (Runnel et al. 2020), even using inoculation of the species (Abrego et al. 2016).

In Europe it follows spruce, occurring in its boreal part and several countries with high mountains (Ryvarden et Melo 2014). In the former Czechoslovakia it was found on old lying logs, rarely on coarse branches, of spruce, exceptionally on fir (Kotlaba 1995). In Slovakia, the only one locality of the species – Dobročský prales (Dobroč Virgin Forest) – had been known for a long time (until 2011). Adamčík et al. (2016) finally revealed another locality for *A. lapponica*, i.e. Klenovský Vepor. Besides data on new records presented in this paper, other public fungaria only have specimens from Dobročský prales.

Holec et Beran (2006) present just one locality in the Czech Republic, from the well-known Boubínský prales (Boubín Virgin Forest), where it only grows on trunks of *Picea abies* (Holec 2019). According to Ryvarden et Melo (2014) this rare species occurs in Europe on dead wood of coniferous trees, usually *Picea abies*, less often *Larix* and *Abies*, and the species is presented as a typical taiga species following spruce with an eastern boreal distribution. According to Alfredsen et al. (2014) it is regarded a strict spruce specialist. Holec et al. (2015b) treat it as a boreal-montane species. Holec et Kučera (2007) noticed that in parts of Central Europe, including Slovakia, it also grows in virgin forest refuges in mixed montane forests mainly composed of *Fagus sylvatica*, *Picea abies* and *Abies alba*. Our data mostly confirmed this fact but does not correspond with Fraiture et Otto (2015), who placed the species in the lowlands or exceptionally lower mountainous regions. All our collections are from higher mountains with the lowest record from an elevation of approximately 700 m. The same can be stated for the one locality in the Czech Republic.

Our results correspond exactly with the conclusions by Fraiture et Otto (2015), who associate *A. lapponica* mainly with *Picea abies*. On the other hand, some collections of *A. lapponica* from *Abies alba* in Slovakia may be questionable, since records from this tree species have not been confirmed recently. It is generally not easy to distinguish fallen trunks of *Abies alba* in ongoing decay

from those of *Picea abies*. Exclusively *Picea abies* is also mentioned as the host of *A. lapponica* by Holec et al. (2015b) from Boubínský prales. Karasiński et Wołkowycki (2015) present exclusively this tree species as the host of *A. lapponica* from Białowieża, the only locality in Poland (Piątek 2005a).

The main fructification period in the former Czechoslovakia was found to be September (Kotlaba 1984), while Fraiture et Otto (2015) mention July to October, Holec (2019) September to November, and Ryvarden et Melo (2014) mention a period late in the season in Europe. Alfredsen et al. (2014) detected mycelia of the species in less decayed parts of wood, Holec et al. (2015b) on fallen trunks in decay stages 2 and 3 out of five, typically without bark (Holec 2019). However, Fraiture et Otto (2015) compiled data on records of fruitbodies on moderately decayed, often still partly corticated trunks, Bader et al. (1995) and Runnel et al. (2020) on medium to well-decayed downed spruce trunks, and Moor et al. (2021) on trunks in an intermediate decay stage.

As mentioned above, the species is known to be highly specialised. It requires a particular type of deadwood (Moor et al. 2021) and grows very preferentially in old-growth forests (Røsok 1998, Kotiranta et al. 2005, Holec et al. 2015b), which has been confirmed by our results. The species is also part of conservation translocations of threatened wood-inhabiting fungi (Nordén et al. 2020), and its local dispersal seems to play an important aspect (Runnel et al. 2020).

Antrodia labyrinthica

There are records from 8 localities of the species (Fig. 3) in Slovakia (Fig. 4). The species occurs in submontane and montane mixed old-growth forests, consisting of different tree species, with different degrees of human influence (Tab. 1). Records are from elevations of 500 to 875 m a.s.l. Fruitbodies were found on 7 fallen trunks exclusively of *Abies alba* in late initial and intermediate stages of wood decay (prevailingly SOD 2) during the whole year.

The species was formerly known as *Antrodia variiformis* in Europe but the distribution of the species with this name is now known to be restricted to North America. Ryvarden et Melo (2017) reclassified *Fomitopsis labyrinthica* to *Antrodia labyrinthica* and *Antrodia kmetii*, a new species recently described (Vlasák et al. 2013) and formerly identified with *A. labyrinthica* (Vampola et Charvátová 2021). The ecology and distribution of these related species are similar. *Antrodia variiformis* appears on dead conifers, mostly on *Picea*, in montane coniferous forests (Spirin et al. 2017), while *A. labyrinthica* occurs on dead wood of *Abies alba* (Ryvarden et Melo 2014).

In Europe, *Antrodia labyrinthica* was formerly only known from northern Italy (Ryvarden et Melo 2014) but Ryvarden et Melo (2017) later mentioned its occurrence in southern Europe – Croatia, France, Italy, Slovakia (disputable

Fig. 3. *Antrodia labyrinthica*, Kremnické vrchy Mts., Badínsky prales NNR, wood of *Abies alba*, 5 March 2014 (PVKU 1185). Photo V. Kunca.

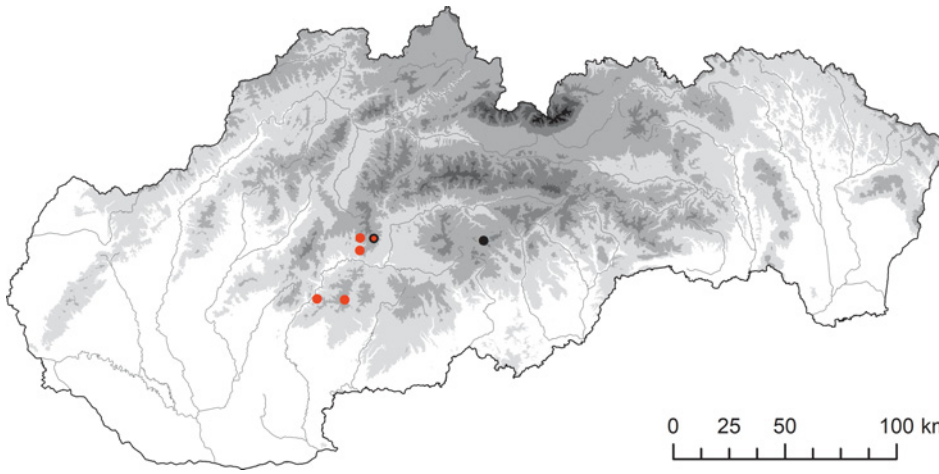

Fig. 4. Distribution of *Antrodia labyrinthica* in Slovakia (8 localities). One dot may represent several closely situated localities. Shaded areas indicate altitudinal zones (up to 300 m, 300–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m and over 2000 m a.s.l. – the darker the area, the higher the elevation). Black dots represent historical records until 2000, red dots recent records since 2001, black-red dots a combination of historical and recent records in the same area.

geographical classification) and Spain. Kotlaba (1985) presented three collections of *A. variiformis* in Czechoslovakia and regarded the species to be extremely rare. Until 2014, specimens from only two Slovak localities were stored in public fungaria.

Kotlaba (1985) mentioned only fir (*Abies alba*) as the substrate of *A. variiformis* in Czechoslovakia. Bernicchia et al. (2007a) classified *Fomitopsis labyrinthica* as a very rare species on fir in Italy. Tortić (1998) included *A. variiformis* into a list of indicator fungi for old forests of beech and fir and associates its occurrence at five localities with wood of *Abies* only. Karadelev et Rusevska (2016) present only one record of *A. labyrinthica* from Macedonia, on fir. Spirin et al. (2017) also associate the species (under name of *A. kmetii*) with fallen trunks of fir, besides *Abies alba* also *A. pinsapo*.

The general occurrence of fruitbodies during the year has probably not been published. In addition, whether its fruitbodies are annual (Ryvarden et Melo 2017) or perennial (Kotlaba 1984) is still unclear and no information has been published in recent literature. Kotlaba (1985) mentioned records from Slovakia from summer to autumn, Vlasák et al. (2013) only from autumn, whereas our collections were made throughout the year.

With regard to the fact that, due to a combination of various factors, *Abies alba* has exhibited a considerable decline at many localities in Europe in recent decades (Holec et Kučera 2020), the survival of *Antrodia labyrinthica* is endangered.

Ionomidotis irregularis

Presently 4 localities of *Ionomidotis irregularis* (Fig. 5) are known in Slovakia (Fig. 6). Records of the species are from submontane and montane old-growth beech-fir and beech forests, two of them virgin forests (Tab. 1). The altitude of the records ranges from 505 to 1005 m. The species was only found on fallen beech trunks in intermediate stage of decay (all 4 records with SOD 3) during autumn.

There were and still are many unresolved molecular and taxonomic uncertainties in the genus *Ionomidotis*, including *I. irregularis* (Pärtel et al. 2017). Most published data on the species is from the USA, where it was originally described (Zhuang 1988). In Europe it was first collected in the Białowieża virgin forest and was, due to absence of published information at that time, described as *Poloniodiscus fischeri* (Svrček et Kubička 1967). However, Zhuang (1988) found this species to be conspecific with *I. irregularis*.

Læssøe et Petersen (2019) regard the species as widespread but rare in central and eastern Europe. The first record of the species in Slovakia was from Stužica NNR, the largest and best-preserved virgin forest in the country (Kuthan

Fig. 5. *Ionomidotis irregularis*, Bukovské vrchy Mts., Rožok NNR, wood of *Fagus sylvatica*, 12 Oct. 2012 (PVKU 798). Photo V. Kunca.

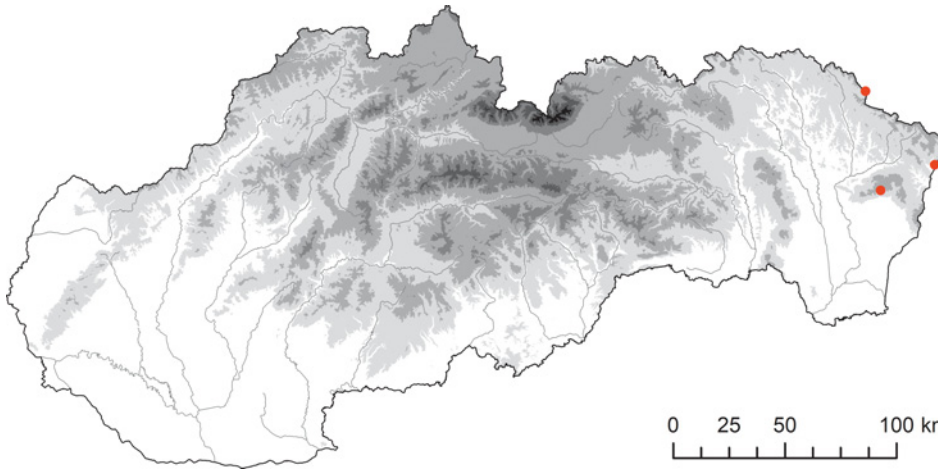

Fig. 6. Distribution of *Ionomidotis irregularis* in Slovakia (4 localities). Shaded areas indicate altitudinal zones (up to 300 m, 300–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m and over 2000 m a.s.l. – the darker the area, the higher the elevation). Red dots represent recent records since 2001, black-red dots a combination of historical and recent records in the same area.

et al. 1999). This record was later confirmed by Adamčík et al. (2007). A collection from the Vihorlat Mts., as the second locality in Slovakia, was published by Adamčík et al. (2016), although it had been mentioned before in Běťák et al. (2012). Similarly, besides new data for Slovakia presented in this paper, only one specimen (Stužica Virgin Forest) is present in public fungaria.

Běťák et al. (2012) analysed 17 localities of the species in Europe. Almost all this data confirmed its occurrence on decayed trunks of broadleaf trees in virgin, natural or near-natural forests. The observed tree species were mainly *Fagus*, others were *Carpinus betulus*, *Betula* sp., *Alnus incana*, *Ulmus glabra* and *Ulmus* sp. Other, more recent records in Europe originate from rotten wood of a deciduous tree (Pärtel et Põldmaa 2008), well-decayed trunks of *Ulmus* sp. and *Betula* sp. (Popov et Arslanov 2014) and *Fagus sylvatica* (Díaz Fernández et al. 2017). The first record in Slovakia was from a well-decayed trunk of *Fagus* (Kuthan et al. 1999), which corresponds with our results. There are three localities of the species in the Czech Republic in all categories of old-growth forests mentioned above (Holec et al. 2015b). The first reports on its occurrence on fallen trunks of conifers, like *Picea abies* and *Abies alba* (Holec 2019, Holec et Kučera 2020), are interesting. Despite long-term research into trunks of *Abies alba* in Slovakia (e.g. Kunca 2016, Kunca in prep.) we have not been able to find the species on this substrate here.

Fructification, as based on different records in the literature (Svrček et Kubička 1967, Zhuang 1988, Pärtel et Põldmaa 2008, Běťák et al. 2012, Díaz Fernández et al. 2017) and our findings presented here, is typically concentrated in autumn.

The species prefers old-growth forests (Holec et al. 2015b), is regarded as their flagship species (Běťák et al. 2012), is proposed to be an indicator of old-growth forests (Huhtinen et al. 2010, von Bonsdorff et al. 2014), and is associated with natural forests (Holec 2019). Our records also confirmed its strict requirements for long-established virgin and natural forests.

Skeletocutis odora

Thirty-two localities of this species (Fig. 7) are known in Slovakia (Fig. 8). The species occurs in submontane to montane old-growth forests, occasionally (3 records) in managed forests (Tab. 1), mixed or homogeneous stands of different tree species. It was recorded from 430 to c. 1270 m a.s.l. on fallen trunks of different tree species, mainly on fir and spruce, occasionally on beech and a non-identified broadleaf tree. Two historical records are from *Alnus*. The fruitbodies can be mainly found in summer and autumn. Twenty-seven of 38 records (i.e. 71%) are from trunks in the intermediate stage of wood decay (SOD 3).

Fig. 7. *Skeletocutis odora*, Veľká Fatra Mts., Maďarovo old-growth forest remnant, wood of *Picea abies*, 18 Sept. 2020 (TMKPVL, MJ 7577). Photo M. Peiger.

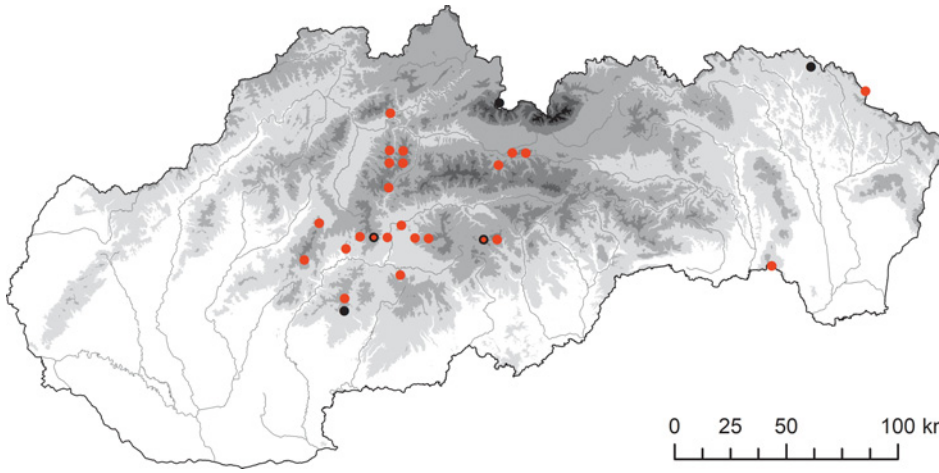

Fig. 8. Distribution of *Skeletocutis odora* in Slovakia (32 localities). One dot may represent several closely situated localities. Shaded areas indicate altitudinal zones (up to 300 m, 300–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m and over 2000 m a.s.l. – the darker the area, the higher the elevation). Black dots represent historical records until 2000, red dots recent records since 2001, black-red dots a combination of historical and recent records in the same area.

Bredesen et al. (1997) classified the species as a strong indicator of old-growth spruce forests with continuity in deadwood. Kotiranta et Niemelä (1993) suggested it to be an indicator of biotic integrity and conservation value for boreal coniferous old-forests. Fraiture et Otto (2015) characterise it as an anthropophobic fungus of natural and near-natural forests, and therefore a good indicator of coniferous virgin forests and mixed forests with conifers. Tortić (1998) considered the species to be indicative of old forests with fir. As mentioned before, Kotiranta et Niemelä (1993) proposed *Skeletocutis odora* as an indicator of old boreal coniferous forests. The species has also been used, as an old-forest species, in habitat suitability modelling (Store et Jokimäki 2003).

It is generally widespread in Europe and usually found in more or less pure virgin forests and old stands in Fennoscandia and prefers old-growth forests (Piątek 2005b, Łuszczyński 2007, Holec et al. 2015b). In the former Czechoslovakia, Kotlaba (1984) mentioned 7 localities of the species – 3 in Czechia and 4 in Slovakia. Over the last decades we can see an apparent increase in the number of sites in Slovakia, just as is stated for the Czech Republic (Fraiture et Otto 2015). However, the species still prefers forests with little human impact. Besides new data presented in this paper, only three specimens are known in Slovak and Czech public fungaria in addition to the already mentioned Dobročský prales and Badínsky prales, also from the Vtáčnik Mts.

Ryvarden et Melo (2014) distinguish its distribution in northern Europe, where it occurs almost exclusively on *Picea*, from central Europe, where it is also found on *Abies*, and southern parts of Europe, where it grows on *Pinus*. Fraiture et Otto (2015) further mention different broadleaf trees. Holec et Beran (2006) mentioned several localities of the species from dead wood of conifers (spruce, fir) and exceptionally also broadleaf trees, Holec et al. (2015b) found the species in Boubínský prales only on *Picea abies* and *Abies alba*. Piątek (2005b) presented five localities of the species in Poland, with the majority of collections on fallen trunks of *Picea abies* in Białowieża virgin forest. Karasiński et Wołkowycki (2015) mentioned occurrence of the species in the Białowieża predominantly on *Picea*, but also on *Pinus*, *Betula* and *Populus*. In another part of Poland, it is associated with fir and spruce trunks (Łuszczyński 2007) and at yet another, new locality it was found on a trunk of *Abies alba* (Chachula 2016). Bernicchia et al. (2007a) listed its occurrence on fir in Italy and classified it as a very rare species. Our results do not exactly correspond with Fraiture et Otto (2015), who mostly associate the species with *Picea abies*. According to Dahlberg et Croneborg (2003) it prefers spruce (*Picea* spp.), but it can also be found on aspen (*Populus tremula*) in coniferous virgin forests. This was confirmed by Markkanen et Halme (2012), who recorded the species during a study in the boreal zone only on broadleaf wood (*Populus*), and locally as very common in aspen forests (Spirin

2005). Volobuev (2013) presents a record from a standing dry trunk of *Populus tremula* in an aspen-birch forest.

In Finland (boreal zone) it prefers large-sized fallen trunks with the bark still attached and a shady and fertile habitat with a humid microclimate (Store et Jokimäki 2003). Similarly, Volobuev (2013) describes its habitat as wet forests undisturbed by human activity. At the eastern border of Europe (Ural Mts.), it can be found on several tree species, such as *Pinus*, *Populus*, *Abies* and *Picea*, in one region (Kotiranta et al. 2007). Fraiture et Otto (2015) reported the species from often decorticated, moderately decayed fallen trunks. Also Běťák (2015) and Holec et Kučera (2020) mostly associate this species with trunks in decay stage 3, which is consistent with our results.

Fruitbodies can be found from summer to autumn (Piątek 2005b), from June to October (Fraiture et Otto 2015), the same periods as those which result from our recent records. However, historical records (Electronic supplement) also originate from May (Kotlaba 1984).

The distance to the nearest old-growth forest can play an important role in the occurrence of wood-inhabiting fungi in managed forests. This could be the case of two records of *Skeletocutis odora* from managed forests (Sielnica and Slanská Huta), which are situated at a distance of up to 5 km from the nearest old-growth forest. In a third case (Kráľová) several fragments of near-natural forests are present in the surrounding. The occurrence of some rare lignicolous fungi in managed forests can moreover be related to the high amount of deadwood in forests in Slovakia. Forest Europe (2015) reports 40.6 $m^3 \cdot ha^{-1}$ of standing and lying deadwood for forests in Slovakia, being the highest average value in Europe.

Yuchengia narymica

Records from 49 localities of this fungus (Fig. 9) are known from Slovakia (Fig. 10). It was found from lowland to montane mixed forests of different tree species with a natural tree composition (170–1102 m a.s.l.) in the whole forest naturalness spectrum – from virgin forests to frequently managed ones, even two times in parks (Tab. 1). These records are predominantly from wood of beech, occasionally hornbeam (*Carpinus*) and individually (1 record) from *Quercus petraea*, *Betula*, *Alnus*, *Sorbus aucuparia* and *Corylus*, over the whole year. Half of the 26 records on trunks concern the late initial stage of wood decay (SOD 2). Several collections are also from snags and branches, one even from the base of a living beech tree.

The species was formerly considered rare (Kotlaba 1995, Kuthan et al. 1999, Vampola et Vágner 2007) or records were only published from old-growth forests (Ordynets et Nadyeina 2013, Adamčík et al. 2016). Together with numerous data from fungaria, almost 50 localities of *Yuchengia narymica* are known in Slovakia

Fig. 9. *Yuchengia narymica*, Štiavnické vrchy Mts., Jabloňovský Roháč NNR, wood of *Fagus sylvatica*, 13 Oct. 2015 (PVKU 1548). Photo V. Kunca.

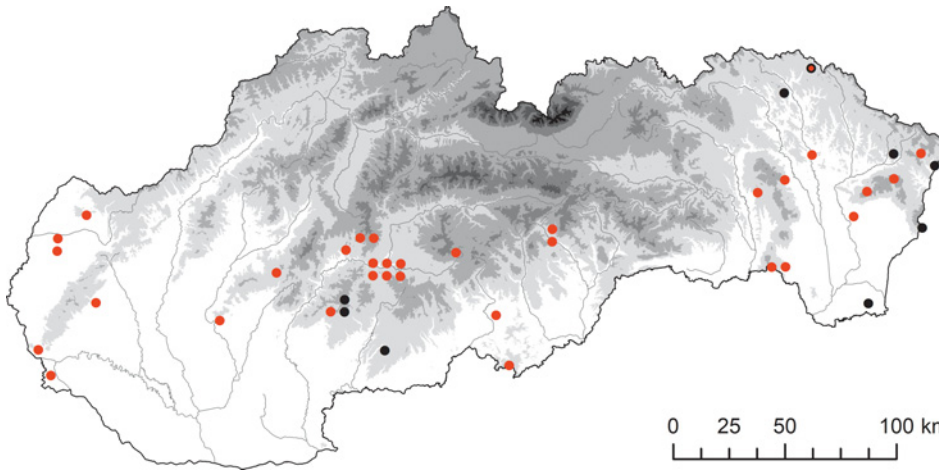

Fig. 10. Distribution of *Yuchengia narymica* in Slovakia (49 localities). One dot may represent several closely situated localities. Shaded areas indicate altitudinal zones (up to 300 m, 300–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m and over 2000 m a.s.l. – the darker the area, the higher the elevation). Black dots represent historical records until 2000, red dots recent records since 2001, black-red dots a combination of historical and recent records in the same area.

today. The species does apparently not prefer only forests which are well-preserved here, but also managed ones whose tree composition is natural or near-natural (Tab. 1).

In Europe, *Yuchengia narymica* occurs in its eastern and southern parts (Ryvarden et Melo 2014). It was formerly known from five localities in Slovakia (Kotlaba 1995), published from different natural forest communities of floodplains, hornbeam-oak, beech and fir-beech forests at elevations of 115 to 750 m a.s.l. Fruitbodies of the species have been found growing on *Carpinus betulus*, *Fagus sylvatica*, *Populus tremula*, *Salix alba* and *Abies alba*. In addition, Vampola et Vágner (2007) presented 15 localities with other tree species as a substrate: *Populus* sp., *Frangula alnus* and *Prunus avium*. In the virgin forests of Havešová and Stužica it was only found on beech, the dominant tree species here (Adamčík et al. 2016). Our data collection adds *Corylus avellana*, *Alnus glutinosa*, *Quercus petraea*, *Betula* sp., *Betula pendula*, *Fraxinus excelsior* and *Populus alba* to this substrate list for Slovakia. Holec et Beran (2006) and Vampola et Vágner (2007) mention only one locality in the Czech Republic on broadleaf deadwood. However, Dvořák et Běťák (2017) recently published several new records of the species in the Czech Republic from different tree species, including *Acer platanoides*, *Quercus petraea*, *Tilia* sp. and *Corylus avellana*.

According to Ryvarden et Melo (2014) the species grows on *Carpinus*, *Eucalyptus*, *Fagus*, *Populus* and *Salix*. In Italy, the species can only be found on conifers (*Pinus* spp.) while it is very often recorded on deciduous wood in the rest of Europe (Bernicchia et al. 2007b). Also a record from *Pinus sylvestris* is known from West Siberia (Filippova et Zmitrovich 2013). Karasiński et Wołkowycki (2015) regard it a very rare Eurasian species associated with deciduous wood and old-growth forests. They also present *Betula pubescens* as the substrate of the species. Another tree species – *Betula verrucosa* (*B. pendula*) – was mentioned by Zhao et al. (2013), the substrate from which it was described.

General data on the fructification of the species is very rare. Kotlaba (1984) presumed a range from June to October for the former Czechoslovakia. Records from our database range from January to November.

Based on a limited number of historical data, recent collections from Slovakia (this paper) and new data from the Czech Republic (Dvořák et Běťák 2017, Vampola et Charvátová 2021), the species is currently expanding.

Conclusion

Processed data on records of five wood-inhabiting fungal species in Slovakia has revealed different and sometimes specific requirements for natural conditions: wood substrate, its stage of decay and forest naturalness. These fungi

thrive in old-growth forests but can also survive in managed forests, especially in stands localised close to forests with high naturalness. From the perspective of biodiversity support, leaving deadwood (also originated from the activity of abiotic factors and biotic actors – windstorms, bark beetles, etc.) and retaining veteran trees at the site are the most important conditions determining the occurrence of wood-inhabiting fungi. Especially in forest ecosystems with a natural tree composition, forest continuity and minimal influence of human activity it is necessary to maintain a certain volume of decaying trunks of different diameters and in various decay stages. The best way, especially in protected areas, is non-intervention management of forests.

The increase in records of some species can be related to more intensive mycological research and a possible expansion of some species. However, regular and broad mycological research in old-growth forests in Slovakia is still insufficient, although the situation is slowly improving in some regions.

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