Hungarian University of Agriculture and Life Sciences

Doctoral School of Biological Sciences

DIVERSITY OF LICHENICOLOUS FUNGI IN CONNECTION WITH THEIR HOST SPECIES AND HABITAT IN HUNGARY

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PhD Thesis

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BACKGROUND AND AIMS OF THE INVESTIGATION

One of the most serious recent problems of mankind is the global level loss of biodiversity in nature. As a result of climate change, the increasingly extreme weather conditions may also make the stability of the habitats known so far uncertain in the future. Cryptogamic organisms, such as lichens and lichenicolous fungi, also need to adapt to changing environmental conditions (FARKAS et al. 2022, MORILLAS 2024), taking into account that the microclimate and microhabitats provide them with opportunities for their colonisation even in dynamically changing conditions (VERES et al. 2021) and although their size is quite small, they can contribute to biodiversity to a large extent.

Lichens are considered as a miniature ecosystem in which a moderated network of relationships develops between diverse groups of organisms, i.e. they can be treated as a holobiome (ASCHENBRENNER et al. 2016, GRUBE et al. 2009, 2012, GRIMM et al. 2021). They are also associated with lichenicolous fungi that are the subject of my thesis as secondary, accessory fungi (Fig. 1). With the progress of molecular genetic studies, knowledge of these has become inevitable, since it does matter where the sample is taken from a lichen thallus, because apart from the fungus that forms the main mass of the lichen, other fungi (lichenicolous) can be identified, even if they are not visible at all on the surface of the lichen thallus (endolichenic fungi).

Lichenicolous fungi form an ecologically highly specialized and successful group within fungi, as they live exclusively on lichens. Most often, they are species-specifically associated with some species and genera of lichen-forming fungi, but there are also pathogens, saprotrophs and commensalists with a wide host spectrum. However, from a systematic point of view, they are not uniform, they have the most diverse morphological and phylogenetic representatives (DIEDERICH et al. 2018, LAWREY & DIEDERICH 2003). Accordingly, extensive mycological knowledge is required for their study.

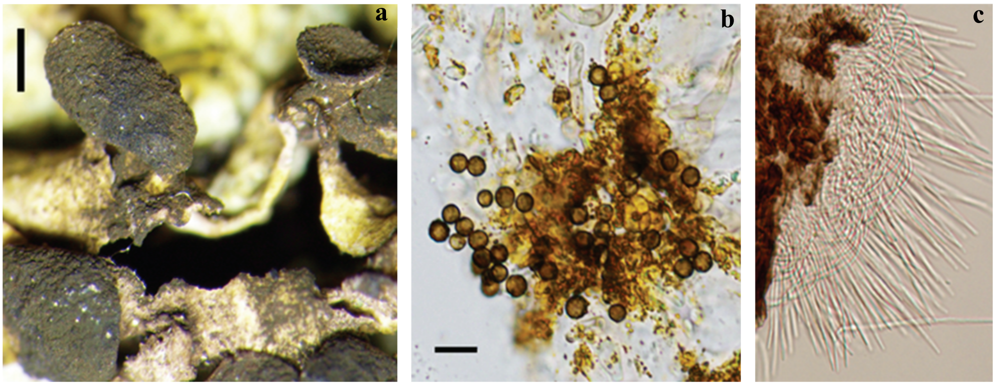

Fig. 1. Some lichenicolous fungi on *Xanthoria parietina*: **a** = *Xanthoriicola physciae* colouring black the host's thallus and apothecia (scale: 500 μm); **b** = brown, globose conidia of *Xanthoriicola physciae* (scale: 10 μm); **c** = hyaline, filiform conidia of *Epithamnolia xanthoriae* (scale: 10 μm)

Hazslinszky was the earliest to publish data on the territory of present-day Hungary, first on *Abrothallus smithii* (HAZSLINSZKY 1859). He was followed by Lojka, Hollós, Kalchbrenner, Sántha, Szatala and Gyelnik, in whose works we also find data on lichenicolous fungi. Szatala describes *Holló-sia vértesensis* as a species new to science from the lichen *Peltigera canina* (KŐFARAGÓ-GYELNIK 1939), the holotype of which is in the BP collection (BP 91043, T 197), and the current name is *Scutula epiblastematica*. BÁNHE-GYI et al. (1985a, b, 1987) includes the works of natural scientists (botanists, lichenologists, mycologists) mentioned above in their work entitled "*Magyar-ország mikroszkopikus gombáinak határozókönyve 1–3.* [*Identification key to the microscopic fungi of Hungary 1–3*]". I made a detailed analysis of the liche-nicolous fungus data in this handbook in my university thesis (VARGA 2009). After that, we can list the names of Diederich, Thor, Verseghy, Farkas, Grube, Hafellner, Lawrey, Lőkös, Šoun, Vondrák as those who mentioned occurrences of different taxa. An important stage was the inclusion of lichenicolous species in the list of LŐKÖS & FARKAS (2009), followed by the compilation of the first separate list of lichenicolous fungi (VARGA et al. 2021).

The basis and core of my PhD thesis is provided by our article entitled "*Annotated checklist of the lichenicolous fungi of Hungary*" published in Diversity in 2021 (VARGA et al. 2021), in which we treated the literature data we could find and specimens placed in collections. The vast majority of our new results originated from our own collections. In my dissertation, I created a revised, extended version of this list adding detailed evaluations. The species are listed in alphabetical order with characterization and remarks on taxonomy, nomenclature, hosts and distribution, and I added an identification key to species.

The aim of my thesis work is therefore

- to prepare a revised list of Hungarian species, which I should supplement with their host species, their habitat data and their most important observed or measured properties, and to give a further assessment of each taxon, where necessary;
- to present the distribution of the most important and relatively data-rich species on maps;
- to use the lichenicolous index (LI) for a large-scale comparison of the relative diversity of Hungarian lichenicolous species with other geographical areas;
- to monitor the presence of lichenicolous fungi in experiments on the extraction and re-production of the lichen secondary metabolites of *Cladonia foliacea*;
- to provide an identification key to species for easy identification.

In order to do this I planned

- to collect and list those species that have already been reported from the country (critically handling data from historical Hungary) as literature data;

- to examine the specimens found in Hungarian herbaria and to carry out the revision, if necessary;
- to screen systematically certain groups of lichen specimens in herbaria (species *Hypocenomyce scalaris*, *Solorina saccata*, *Varicellaria lactea*, *Xanthoria parietina*, genera *Cetraria*, *Cetrelia*, *Cladonia*, *Lepraria*, *Parmelia*, *Xanthoria* s. l.), where lichenicolous fungi are most likely to occur;
- to collect lichenicolous fungi or lichen thalli characteristic as host species on purpose during my fieldwork;
- to deposit voucher specimens in the BP and VBI lichen collections.

MATERIALS AND METHODS

I studied collections of 13 herbaria (BP, CBFS, DE, EGR, GODU, JPU, M, PRA, S, SAMU, SZE, VBI, W) for lichenicolous fungi. I examined nearly 3,000 specimens of 8 herbaria (BP, DE, EGR, GODU, JPU, SAMU, SZE, VBI), among which 300 came from my own collection. The species list included those taxa that were supported by a specimen (or specimens) and were verified to have occurred on lichens in Hungarian or foreign herbaria.

For the identification of the host lichen species and lichenicolous fungi, identification keys by DIEDERICH et al. (2022), IHLEN & WEDIN (2008), HAWKSWORTH et al. (2010), SMITH et al. (2009), VERSEGHY (1994), WIRTH et al. (2013) were consulted. Wherever possible, I took into account the “one mushroom – one name” principle (cf. HAFELLNER 2018).

Concerning to nomenclature, similarly to the list of LŐKÖS & FARKAS (2009) Index Fungorum (IF) (CABI 2024) and MycoBank (MB) are followed mainly, but DIEDERICH et al. (2018, 2022), furthermore HAWKSWORTH (1983), HAWKSWORTH et al. (2010), IHLEN & WEDIN (2008), KOCOURKOVÁ (2000), NASH et al. (2004, 2007), SANTESSON et al. (2004), and ZHURBENKO & PINO-BODAS (2017) were also consulted. In the case of the host species, the author names are found in the IF and MB databases, I indicate them only for species of lichenicolous fungi.

During my research, I used classical microscopic morphological methods. I examined the habitus of host lichens and lichenicolous fungi with a stereomicroscope (Olympus SZX9, Nikon SMZ18), and also examined preparations of hand sections (c. 5,000) covered in water with different reagents and dyes (PD, K, Cl, K/I, N, cotton blue, Congo red) in a research microscope (Olympus BX50, NIKON Eclipse/NiU). To take microphotos, I used an Olympus E450 reflex camera (with Quick Photo Camera 2.3 software) and Nikon DS-Fi1c and Fi3 digital cameras equipped with NIS-Elements BR ML software. The lichen secondary metabolites were identified using the HPTLC chemical analytical method. I created the distribution maps with the computer program QGIS 3.18.2 "Zürich", 2020.

According to ZHURBENKO (2007), the lichenicolous index (LI) is the ratio of lichenicolous fungal species and lichen species in a given area.

Experiments (2017–2020) on the acetone extraction and re-production of lichen secondary metabolites (usnic acid and fumarprotocetaric acid) of the lichen *Cladonia foliacea* were aimed at the dynamics of the re-production of these lichen materials (VERES et al. 2022). Thalli from lowland sand steppe (Vácrátót, Tece) and mountain dolomite rocky grassland (Bakony, Sóly) habitats were exposed to open field (Centre for Ecological Research, Vácrátót) long-term experiments. Since lichen secondary metabolites produced in the studied lichens can influence the appearance of lichenicolous fungi (ASPLUND et al. 2018, LAWREY 2000), their occurrence was recorded every six months by marking presence/absence (+/–) or simple change in abundance (+, ++, +++) for each treatment. In the case of mature lichen thalli, the most common species were determined.

RESULTS AND DISCUSSION

The latest list of lichenicolous fungi in Hungary contains 110 species, all of which I confirmed and supported with herbarium specimens. I deposited new specimens of 97 species in collections (BP, VBI) and confirmed the presence of additional species on previously deposited collection materials, and collected data of nearly 800 specimens.

I listed the host lichens, thus showing that the 110 lichenicolous fungi colonise at least 83 species of host lichens in Hungary. From these, 50 species living in Hungary, I have identified only one species of lichenicolous fungus. I identified two lichenicolous species from 15 host lichens, three lichenicolous fungi from *Cladonia pyxidata*, *Diploschistes scruposus*, *Squamarina cartilaginea* and *Xanthoparmelia conspersa*, four lichenicolous species from six lichens, five from *C. foliacea*, *Hypogymnia physodes*, *Parmelia sulcata* and *Solorina saccata*, six from *C. magyarica* and *Lecanora* sp., ten from *Physcia adscendens* and the largest number, 18 lichenicolous species, from *Xanthoria parietina*.

Among host lichens, the genera *Cladonia* and *Lecanora* are listed with 7–7 species, and the Physciaceae family with 10 species. Lichens containing cyanobacteria, which do not or contain few lichen secondary metabolites, appear in low numbers in the list. Of the *Peltigera* species, 4 are listed at the species level and one at the genus level, with 1–2 distribution data, and the same applies to the former *Collema* and *Leptogium* species as well. *Peltigera* species usually form a large thallus and thereby provide enough surface area for the establishment of lichenicolous fungi, and the small number of their secondary metabolites can represent fewer limiting factors for the establishment of parasites (LAWREY & DIEDERICH 2003, MOLNÁR & FARKAS 2010).

Along with *Xanthoria parietina*, *Physcia adscendens* and *Phaeophyscia orbicularis* are the most common lichens in the lichen communities present in anthropogenic environments, and I managed to detect the largest number of lichenicolous fungi from these species (*P. adscendens* – 10, *X. parietina* – 18).

In addition, I also identified a relatively large number of 5 lichenicolous fungi from Hungarian specimens of the protected *Solorina saccata* species (FARKAS et al. 2022b), which is retreating due to the threat of its habitat. Furthermore 6 lichenicolous fungi were identified from the also protected *Cladonia magyarica*.

Athelia arachnoidea and *Xanthoria parietina* are situating at the two extreme ends of the lichenicolous fungus and host lichen lists. *A. arachnoidea* is a parasite with a broad host spectrum, which not only attacks lichens, but also lives on mosses, free-living algae, tree bark and leaves, and I have identified 19 lichen species from different parts of the country. They are among the lichenicolous fungi living on *Xanthoria parietina*, which I have only shown from one place or another (e.g. *Capronia suijae*, *Pleospora xanthoriae*, *Pseudorobillarda xanthoriae* ad int.), while *Xanthoriicola physciae*, which only parasitizes this lichen, has been found in almost every part of the country, and sometimes as a dominant parasite is present. The species *A. arachnoidea* and *X. physciae* are the most common lichen parasites in the country, this is supported by the points marked on the distribution maps (Fig. 2) and the specimens in the collection, supplemented by detection data, which we do not record due to the frequency of the species.

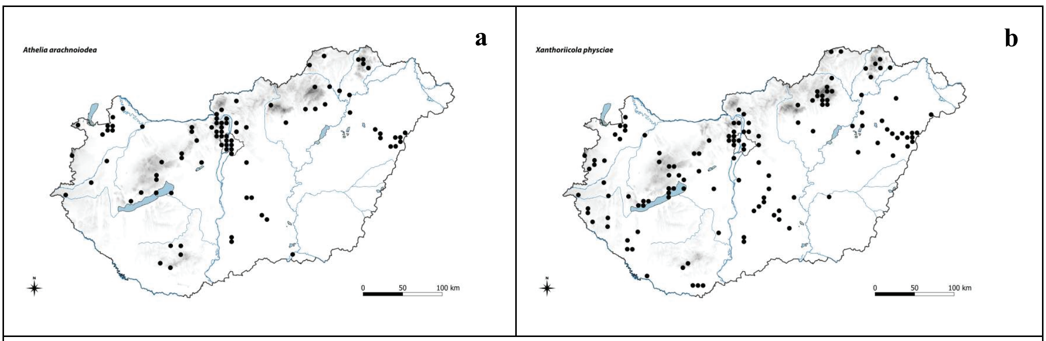

Fig. 2. Distribution maps of lichenicolous fungi: **a** = *Athelia arachnoidea*, **b** = *Xanthoriicola physciae*

Based on the lichenicolous index (LI) values, we can conclude that the knowledge on Hungarian lichenicolous fungi is somewhat higher than the value calculated for the world (Table 1).

Table 1. Lichenicolous Index (LI) values by country and region, by number of lichen and lichenicolous fungi species

Country or Region	Lichenicolous Fungi	Lichens	Lichenicolous Index (LI)
Bavaria (Germany)	399	1624	0,246
Great Britain	384	1677	0,229
Belgium, Luxemburg, N France	201	930	0,216
Germany	392	1946	0,201
Italy	492	2565	0,192
France 2020	592	3185	0,186
Fennoscandia	430	2387	0,180
France 2017	546	3082	0,177
France 2014	513	3528	0,145
USA, Canada	631	4880	0,129
Ukraine	246	1910	0,129
Hungary 2024	110	954	0,115
Hungary 2021	104	926	0,112
World	2000	19387	0,103
Albania	38	398	0,095
Russia	276	3388	0,081
Greece	64	1353	0,047
Bulgaria	45	1120	0,040
Romania	40	1194	0,034
Serbia	15	668	0,022

Based on our investigations, the lichens collected for the long-term lichen secondary metabolite reproduction experiment could already be infected with lichenicolous fungi at the time of transplantation. The changes possibly due to the infection (necrotic spots and black bands around) were first observed on the lobe ends (approx. 0.5 cm^2) (Fig. 3a), and later on the surface of the thalli as larger contiguous spots (Fig. 3b), and over time even entire thalli were colonized. The lichenicolous fungus *Didymocyrtis cladoniicola* was found in both control and acetone-treated thalli from lowland or mountain habitats. The lichenicolous fungus *Syspastospora cladoniae* occurred only in one of the lowland control thalli, it was not observed in the treated samples.

Fig. 3. Treated and transplanted thalli of *Cladonia foliacea*: **a** = necrotic lesions on the lobe ends; **b** = discoloration of the entire colony (VERES et al. 2022, Fig.1a-b)

There are lichen genera for which we do not yet have lichenicolous data, e.g. *Ramalina*, *Usnea*, many saxicolous (rock-inhabiting) lichens, so more attention should be paid to these lichens in the future.

The 110 species of lichenicolous fungi can be classified into two fungal phyla, of which 102 belong to Ascomycota and 8 to Basidiomycota. Among the ascomycetes, 50 belong to the Dothideomycetes, 13 to the Sordariomycetes, 12 to the Eurotiomycetes, 11 to the Arthoniomycetes, 4 to the Lecanoromycetes and 2 to the Leotiomycetes, while the position of 10 is uncertain at the class level. Among the basidiomycetes, 6 belong to the class Agaricomycetes, and 2 belong to the class Tremellomycetes (Fig. 4).

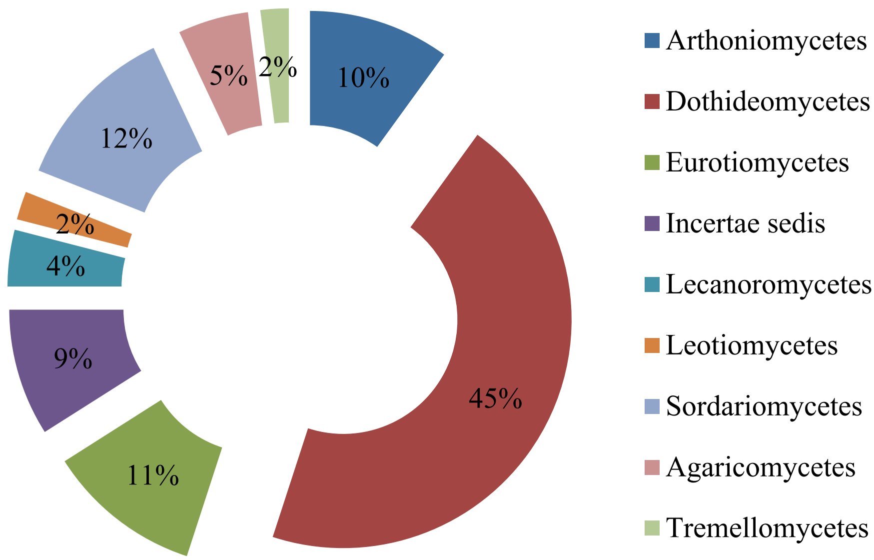

Fig. 4. % distribution of Hungarian lichenicolous fungi in the classes of Fungi

At generic level, *Stigmidium* (10), *Lichenoconium* (7), *Abrothallus* (6), *Didymocyrtis* and *Lichenostigma* (5–5) are represented by larger species number. Genera with a single species only are *Apiosporella*, *Arthonia*, *Athelia*, *Burgoa*, *Capronia*, *Chaenothecopsis*, *Cladoniicola*, *Cladosporium*, *Clypeococcum*, *Didymellopsis*, *Endococcus*, *Epicladonia*, *Epithamnolia*, *Erythricium*, *Gonatophragmium*, *Illosporiopsis*, *Karschia*, *Knufia*, *Laetisaria*, *Lichenodiplis*, *Lichenopuccinia*, *Lichenosticta*, *Lichenothelia*, *Marchandiomyces*, *Monodictys*, *Nectriopsis*, *Opegrapha*, *Penttilamyces*, *Phaeoseptoria*, *Phaeospora*, *Plectocarpon*, *Pleospora*, *Pyrenidium*, *Pyrenochaeta*, *Rhagadostoma*, *Roselliniella*, *Sagedia*, *Sarcopyrenia*, *Spirographa*, *Syspastospora*, *Talpapellis*, *Telogalla*, *Thelocarpon*, *Vouauxiella*, *Weddellomyces*, *Xanthoriicola* and *Zwackhiomyces*.

During field transplantation experiments carried out by dissolving lichen secondary metabolites (fumarprotocetraric acid, usnic acid) in acetone, we identified the *Phoma*-like conidial form of the parasitic species *Didymocyrtis cladoniicola* from thalli of *Cladonia foliacea*. At the end of the experiments (after 3 years), the lichenicolous fungus was clearly and noticeably present in the treated population (VERES et al. 2022), and we came to the conclusion that lichen secondary metabolites can have a regulatory role in the establishment and spread of other organisms, such as lichenicolous fungi, within the lichen thalli and by the death and brittleness of certain parts of the thalli also between the thalli.

The identification key related to the list of lichenicolous fungi reported from the territory of Hungary contains 133 species. It also includes species for which we only have literature data, but whose occurrence is expected. The key has a modular structure and is divided into four major parts: in a separate section there are those that produce apothecium (38 species), another section of the species that produce closed ascoma, i.e. perithecium (53), and in other parts are the basidiomycetes (8) and the conidia-forming ascomycetes (41), those forming a somewhat structured (closed) fruiting body, and species that do not form a fruiting body. Here, five *Abrothallus* species (*A. acetabuli*, *A. caerulescens*, *A. microspermus*, *A. parmeliarum*, *A. prodiens*), *Didymocyrtis slaptonensis* and *Scutula tuberculosa* species are included in two parts of the identification key, as their conidial shape is characteristic or occurs frequently, and due to the rule of one name – one fungus in the Botanical Code (International Code of Nomenclature for algae, fungi, and plants), the relationship of the sexual and asexual forms previously given separate names was confirmed by molecular phylogenetic studies, and according to the rules of the Code, they were given a valid name. This rule came into effect under Section 59 of the Melbourne Code (MCNEILL et al. 2012). Among Hungarian species, such is the case of *Abrothallus microspermus*, where Hungarian specimens are present in conidial form, as its common form, and it was described as *Vouauxiomyces truncatus*. It was later proven to be the same as *A. microspermus*, which occurs alongside it in many cases (PÉREZ-ORTEGA et al. 2011)

NEW SCIENTIFIC RESULTS

1. I have compiled a revised species list of the 136 species of lichenicolous fungi in Hungary.

2. To identify the 133 species of lichenicolous fungi, I was the first to compile an identification key based on Hungarian data.

3. I identified 86 species of lichenicolous fungi as new to Hungary, thereby establishing new data on their distribution. Of these, I was the first to indicate the new occurrence of 33 species of lichenicolous microfungi in Hungary compared to the list published in 2021: *Abrothallus acetabuli*, *Apiosporella caudata*, *Bryostigma epiphyscium*, *Chaenothecopsis parasitaster*, *Cladosporium licheniphilum*, *Didymellopsis pulposi*, *Didymocyrtis physciae*, *Endococcus collematis*, *Gonatophragmium lichenophilum*, *Intralichen lichenum*, *Knufia peltigerae*, *Laetisaria lichenicola*, *Lichenochora weillii*, *Lichenoconium aeruginosum*, *Lichenoconium lichenicola*, *Lichenostigma dimelaenae*, *Lichenostigma maureri*, *Nectriopsis rubefaciens*, *Neolamya xanthoparmeliae*, *Opegrapha physciaria*, *Phaeoseptoria peltigerae*, *Phaeospora squamarinae*, *Pronectria oligospora*, *Pseudorobillarda peltigerae*, *Pseudorobillarda xanthoriae* ad int., *Pyrenidium aggregatum*, *Rhagadostoma brevisporum*, *Sagedia engeliana*, *Spirographa lichenicola*, *Stigmidium cladoniicola*, *Stigmidium hageniae*, *Taeniolella punctata*, *Weddellomyces xanthoparmeliae*.

4. I detected *Pseudorobillarda xanthoriae* N. Varga, Etayo et F. Berger, ad int. from Hungarian specimens of *Xanthoria parietina*, and it is currently under publication process as a species of lichenicolous fungus new for science.

5. I have confirmed the occurrence of 7 species of lichenicolous fungi in Hungary based on recent collections of the species, those were earlier known only from literature data or specimens deposited in not Hungarian collections.

6. I placed nearly 300 Hungarian specimens of 97 species of lichenicolous fungi in public collections (BP, VBI). In addition, within the Budapest (BP) lichen collection, I created a comparative lichenicolous microfungi collection of 200 species from Hungarian and foreign specimens, which serves as a reference material for easier species identification.

7. Based on more than 400 identified herbarium specimens, I created a database containing the locality data of old and recent collections (about 120 years/1904–2024) consisting of 500 records, which is the current most important knowledge base of the distribution of the species of lichenicolous fungi in Hungary.

8. I was the first to use the lichenicolous index (LI) in relation to Hungarian species. In this way, I introduced an indicator value that indicates a global correlation between lichen and lichenicolous fungus diversity in habitats with different environmental conditions.

9. During the 3 years acetone-rinsing and re-production experiments (removing the lichen secondary metabolites usnic acid and fumarprotocetraric acid) of *Cladonia foliacea* thalli, a difference between the infection of the lichenicolous fungi (*Didymocyrtis cladoniicola*, *Syspastospora cladoniae*) in the treated and the control populations was demonstrated.

CONCLUSIONS, RECOMMENDATIONS AND PERSPECTIVES

The knowledge of lichenicolous fungi has increased significantly during the last two decades. In the case of several taxa (e.g. *Erythricium aurantiacum*, *Zyzygomyces* species), it has been confirmed that the presence of more and more species can be detected by increasing field sampling in Hungary.

The appearance and availability of better resolution microscopes can also play a big role. This made it possible to detect, for example, the *Knufia peltigerae* species, which has a small perithecium (100 µm in diameter), and often only the spines around the mouth of the fruiting body sunk into the host thallus are visible to our eyes at a fairly high magnification (50–60×).

Although in many cases the international literature denies a close (species-level) parasite-host relationship, the systematic examination of the host lichen species often leads to the detection of typical lichenicolous fungal species (e.g. finding *Clypeococcum hypocenomycis* on the lichen *Hypocenomyce scalaris* and *Stigmidium eucline* on *Varicellaria lactea*).

A future better understanding of the relationship between lichenicolous fungi and host lichen species in Hungary needs appropriate lichen sampling for molecular genetic studies. In such cases, a detailed microscopic examination of lichen thalli is recommended to exclude parts of thalli containing lichenicolous fungi.

The lichenicolous index (LI) indicates an indicator value for a given country, but it can also be applied to characterize smaller geographical units and biotopes. The value of the index is influenced by how intensively was the area investigated by lichenologists, and how detailed the researchers identified the lichens as host species and potential host species at the examined area.

The extraction of the lichen secondary metabolites has a long-term effect on the appearance of lichenicolous fungi, as the acetone treatment allowed the fungus to spread more easily in the lichen thallus if the level of usnic acid in the bark and fumarprotocetaric acid in the medullary layer decreased.

In the field experiment, not only the extraction of lichen secondary metabolites, but also the transplantation itself could have an effect on the appearance of lichenicolous fungi, possibly causing a small change beneficial to the growth of the fungus. The increased growth of lichenicolous fungi may be partly a consequence of the disturbance caused by the transplantation.

LIST OF PUBLICATIONS PROVIDING THE BASIS OF THE THESIS

Published papers in refereed journals

SINIGLA, M., LŐKÖS, L., VARGA, N., FARKAS, E. (2015): Distribution of the legally protected lichen species *Cetraria islandica* in Hungary. In: *Studia botanica hungarica* 46(1) 91–100

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FARKAS, E., LŐKÖS, L., PAPP, B., SINIGLA, M., VARGA, N. (2016): Zuzmók és mohák biodiverzitás-vizsgálata a szigligeti Kongó-rétek mintaterületen. (Biodiversity of bryophytes, lichen-forming and lichenicolous fungi on "Kongó Meadows" (Hegymagas–Szigliget, Hungary)). In: *Folia Musei Historico-Naturalis Bakonyiensis* 33 19–33

MATUS, G., SZEPESI, J., RÓZSA, P., LŐKÖS, L., VARGA, N., FARKAS, E. (2017): *Xanthoparmelia mougeotii* (Parmeliaceae, lichenised Ascomycetes) new to the lichen flora of Hungary. In: *Studia botanica hungarica* 48(1) 89–104

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VARGA, N., LŐKÖS, L., FARKAS, E. (2021): Annotated checklist of the lichenicolous fungi of Hungary. In: *Diversity (Basel)* 13 557

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