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Diversity of aphyllophoroid fungi from taxonomical and biogeographical perspectives

by
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ABSTRACT

Comprehensive knowledge of biodiversity is a prerequisite for its long-term conservation and sustainable use. Fungi play crucial roles in ecosystems and are among the species-richest organism groups on Earth. However, all aspects of their diversity remain underexplored.

In this study, we aimed to fill the gaps in occurrence data and taxonomy as well as in understanding spatial diversity patterns of aphyllophoroid fungi (non-gilled macroscopic Basidiomycota). We digitized and made openly accessible 4,041 records of aphyllophoroid fungi from Central and Eastern Europe and several tropical areas. Numerous specimen records were associated with newly generated nuclear ribosomal DNA sequences (74 of ITS regions and 59 of 28S region) and numerous observations also with photographs depicting diagnostic features of fungal fruitbodies.

We described 13 new species of aphyllophoroid fungi based on morphological examination combined with DNA barcoding and phylogenetic Bayesian and Maximum likelihood analyses using ITS and 28S DNA sequences. Two new species belong to the genus *Trechispora* P. Karst. and eleven to the genus *Subulicystidium* Parmasto. In the latter, species-level variation in basidiospore size and shape was re-evaluated based on systematic measurements of 2,840 spores from 67 sequenced specimens. An updated identification key to all known species of *Subulicystidium* was provided. Using DNA-based evidence, in the studied lineage (Trechisporales K.H.Larss.) we showed for the first time a possibility of a transoceanic distribution.

Based on a dataset consisting of 14,030 fruitbody occurrences of 1,491 aphyllophoroid fungal species from 39 European areas, we showed that importance of biogeographical regions in determining European aphyllophoroid fungal communities varies for different diversity components. Species richness and nestedness were best explained by European biogeographical regions, whereas overall beta-diversity and species turnover were driven mostly by variation in climate, and nestedness mostly by tree species occupancy. Beta diversity patterns of aphyllophoroid fungi did not differ between southern and northern Europe. Therefore, at the continental scale, aphyllophoroid fungi are less shaped by historical legacies than vascular plant and animal communities.

Keywords: Agaricomycetes, beta diversity, biodiversity informatics, biometry, biogeography, distribution, *Hydnodontaceae*, nestedness, new species, species delimitation, species richness, species turnover, taxon occurrence, taxonomy

ABSTRACT IN GERMAN / ZUSAMMENFASSUNG

Umfassendes Wissen über die Biodiversität ist eine Voraussetzung für ihre langfristige Erhaltung und nachhaltige Nutzung. Pilze spielen eine wichtige Rolle in Ökosystemen und gehören zu den artenreichsten Organismengruppen auf der Erde. Jedoch sind noch nicht alle Aspekte ihrer Vielfalt vollständig erforscht.

In dieser Studie haben wir uns zum Ziel gesetzt, die Lücken in den Verbreitungsdaten und der Taxonomie sowie im Verständnis der räumlichen Diversitätsmuster von aphyllophoroiden Pilzen (makroskopische Nichtblätterpilze der Basidiomycota) zu füllen. Wir haben 4,041 Datensätze von aphyllophoroiden Pilzen aus Mittel- und Osteuropa und verschiedenen tropischen Gebieten digitalisiert und veröffentlicht. Zahlreiche Herbarbelege wurden durch neu erzeugte nukleäre ribosomale DNS-Sequenzen (74 der ITS-Region und 59 der 28S-Region) sowie Fotografien, und diagnostischen Merkmalen zur Artbestimmung von Pilzfruchtkörpern zeigen, ergänzt.

Wir haben 13 neue Arten von aphyllophoroiden Pilzen beschrieben basierend auf morphologischen Untersuchungen in Kombination mit DNA-Barcoding und phylogenetischer Bayesian und Maximum-Likelihood-Analysen von ITS und 28S DNA-Sequenzen. Zwei neue Arten gehören zur Gattung *Trechispora* P. Karst. und elf zur Gattung *Subulicystidium* Parmasto. Im letzteren Fall wurde die Variation der Größe und Form der Basidiosporen auf Artebene neu bewertet, basierend auf systematischen Messungen von 2,840 Sporen von 67 sequenzierten Proben. Ein aktualisierter Identifizierungsschlüssel für alle bekannten Arten von *Subulicystidium* wurde bereitgestellt. Mittels DNA-basierter Evidenz zeigten wir in der untersuchten Linie (Trechisporales K.H.Larss.) erstmals die Möglichkeit einer transozeanischen Verbreitung innerhalb von Arten.

Basierend auf einem Datensatz, der aus 14,030 Fruchtkörpervorkommen von 1,491 aphyllophoroiden Pilzarten aus 39 europäischen Gebieten besteht, haben wir gezeigt, dass der Einfluss von biogeographischen Regionen bei die Bestimmung europäischer aphyllophoroider Pilzgemeinschaften für verschiedene Diversitätskomponenten variiert. Artenreichtum und Nestedness ließen sich am besten durch europäische biogeografische Regionen erklären, während die gesamte Beta-Diversität und der Artenumsatz hauptsächlich durch Klimaschwankungen verursacht wurde, und die Nestedness hauptsächlich durch die Besiedlung der Baumarten bestimmt wurde. Die Beta-Diversitätsmuster von aphyllophoroiden Pilzen unterschieden sich nicht zwischen Süd- und Nordeuropa. Daher sind aphyllophoroide Pilze auf kontinentaler Ebene weniger durch historische Vermächtnisse geprägt als durch vaskuläre Pflanzen- und Tiergemeinschaften.

Schlüsselwörter: Agaricomycetes, Beta-Diversität, Biodiversitätsinformatik, Biometrie, Biogeographie, Verbreitung, Hydnodontaceae, Nestedness, neue Arten, Artenabgrenzung, Artenreichtum, Artenumsatz, Taxonvorkommen, Taxonomie

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to in the text by their Roman numerals:

I. Ordynets A, Savchenko A, Akulov A, Yurchenko E, Malysheva V, Kõljalg U, Vlasák J, Larsson K-H, Langer E (2017) Aphyllophoroid fungi in insular woodlands of eastern Ukraine. Biodiversity Data Journal 5: e22426. doi: 10.3897/BDJ.5.e22426

II. Ordynets A, Larsson K-H, Langer E (2015) Two new *Trechispora* species from La Réunion Island. Mycological Progress 14: 113. doi: 10.1007/s11557-015-1133-0

III. Ordynets A, Scherf D, Pansegrau F, Denecke J, Lysenko L, Larsson K, & Langer E (2018) Short-spored *Subulicystidium* (Trechisporales, Basidiomycota): high morphological diversity and only partly clear species boundaries. MycoKeys 35: 41-99. doi: 10.3897/mycokeys.35.25678

IV. Ordynets A, Heilmann-Clausen J, Savchenko A, Bässler C, Volobuev S, Akulov O, Karadelev M, Kotiranta H, Saitta A, Langer E, Abrego N (2018) Do plant-based biogeographical regions shape aphyllophoroid fungal communities in Europe? Journal of Biogeography 45: 1182–1195. doi: 10.1111/jbi.13203

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III. Ordynets A, Scherf D, Pansegrau F, Denecke J, Lysenko L, Larsson K, & Langer E (2018) Short-spored *Subulicystidium* (Trechisporales, Basidiomycota): high morphological diversity and only partly clear species boundaries. MycoKeys (accepted).

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IV. Ordynets A, Heilmann-Clausen J, Savchenko A, Bässler C, Volobuev S, Akulov O, Karadelev M, Kotiranta H, Saitta A, Langer E, Abrego N (2018) Do plant-based biogeographical regions shape aphyllophoroid fungal communities in Europe? Journal of Biogeography 45: 1182–1195. doi: 10.1111/jbi.13203

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INTRODUCTION

Fungal perspective on biodiversity knowledge

Knowledge on how biodiversity distributed on Earth is crucial for its long-term conservation and sustainable use. This information allows prioritization of conservation actions and guides policy making (Kremen et al. 2008, Meyer et al. 2015). Biodiversity data serves as an input for modelling the distribution of species of interest, which may be a pest or medically important species (Sutherst 2014, van Andel et al. 2015). There is a clear dependency between biodiversity loss and ecosystem resistance to climate extremes (Isbell et al. 2015). Therefore knowledge of biodiversity is of a special importance in the rapidly changing world (Newbold et al. 2015).

To understand how biodiversity changes in space and time, biodiversity data should be properly documented. The FAIR principles to scientific data management—Findability, Accessibility, Interoperability, and Reusability—are fully applicable to biodiversity information (Wilkinson et al. 2016, Penev et al. 2017). Possibilities to digitise the taxon occurrences during the few last years have been additionally improved, providing great benefits for all biodiversity researchers (Abarenkov et al. 2010, Senderov et al. 2016). Nevertheless, a large amount of biodiversity information remains undiscovered or unlocked for public use (Wetzel et al. 2018). There are spatial, temporal and taxon-dependent differences in the availability of biodiversity information (Amano et al. 2016). All these data gaps hamper conservation efforts and benefits from using biodiversity (Meyer et al. 2015).

Members of the Fungi kingdom are efficient mutualists, pathogens, and decomposers, and they serve as key drivers of the carbon cycle. Fungi strongly affect ecosystem functioning, as well as humans and human-related activities (Desprez-Loustau et al. 2007, Clemmensen et al. 2013). However, their diversity remains poorer explored than in animals and plants. This is related to the difficulties of species detection, identification and delimitation. Although it is possible to record fungi from vegetative structures (i.e. mycelia) and dormant propagules (i.e. spores), so far, recording fungal species from reproductive structures (i.e. fruitbodies) has remained the most popular method to inventory macrofungi (Halme et al. 2012). However, fungal fruiting can be irregular and fruitbodies, when available, often persist for a short period of time. Morphological identification of fungal specimens may be time consuming because it requires accounting for a large number of microscopic characters (Bernicchia and Gorjón 2010). Furthermore, reporting the size variation of the key diagnostic structures in mycology (e.g. spores) has not been standardized, and intra-individual, intraspecific and interspecific size variation have often been confused thus hampering species delimitation (Parmasto et al. 1987).

Diversity of fungi is not evenly explored across the globe (Blackwell 2011). Europe is the continent with the most advanced knowledge of fungal diversity, due to a long tradition of research in fungal taxonomy and biodiversity (Mueller et al. 2007, Dahlberg et al. 2010). Numerous national projects and their cooperation enabled researchers to shed a first light onto important ecological processes such as species- and community-level responses of fungi to global warming (Kauserud et al. 2012, Andrew et al. 2016). High data availability results also in the most developed strategies of fungal conservation as exemplified by the Northern European countries (Heilmann-Clausen et al. 2015). In the last years, information on fungal diversity in North and South America has been rapidly accumulated (Rosenthal et

al. 2017, Truong et al. 2017). This data provided important insights into ecology and evolutionary history of fungi but also showed that a substantial part of species lacks scientific names and are yet to be described.

Dimensions of fungal diversity

Fungi are among the species-richest organism groups on Earth (Blackwell 2011, Mora et al. 2011, Larsen et al. 2017). During the last four decades, in average, about 1,300 new species names were introduced each year. Since 2010, this number increased to around 1,800 species per year (Hibbett et al. 2011, Hawksworth and Lücking 2017). Nevertheless, the global fungal diversity remains largely unknown. While ca. 120,000 species of fungi are described to date, the estimates of global species richness vary between 0.5 and 10 million (Hawksworth & Lücking 2017).

As with the number of known species, the number of species occurrences of fungi lags behing the data for animals and plants. In the main biodiversity data aggregator GBIF, the number of registered species occurrences of fungi is 14,564,448. This number is 15 times lower than the number of plant records and 50 times lower than the number of animal records (GBIF.org 2018, accessed on 17 May 2018). The GBIF data currently reflects occurrences as recorded from the morphological structures (fruitbodies in the case of fungi) but the algorithm to represent molecular (DNA) evidence of species presence is under development (Schigel et al. 2017).

Molecular information plays an increasingly big role in mycology. The internal transcribed spacer (ITS) of the nuclear ribosomal DNA is the first choice in taxonomic, evolutionary and ecological studies on fungi since almost three decades (Kõljalg et al. 2013, Hibbett et al. 2016). The ITS has become the official DNA barcode for fungi after showing the best performance for species delimitation on a large spectrum of fungal lineages (Schoch et al. 2012). Therefore the majority of currently available pubic DNA sequences of fungi represent ITS region (Begerow et al. 2010, Nilsson et al. 2017).

The most comprehensive account of ITS sequences of fungi is given by the UNITE database which considers also all sequences from the International Nucleotide Sequence Database Collaboration, INSDC (Kõljalg et al. 2013). The latest statistics shows there is 817,130 public fungal ITS sequences obtained through Sanger sequencing (UNITE version 7.2, last updated 1 Dec 2017, accessible from: https://unite.ut.ee/). There are 1000 times more fungal ITS reads obtained via high-throughput sequencing (Hawksworth and Lücking 2017). However, they are currently not used in the taxonomic workflows but can be accessed via the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/sra).

Grouping current ITS sequences obtained through Sanger sequencing based on a classical 3% dissimilarity threshold (Begerow et al. 2010) results in 51,798 entities called "Species Hypotheses" (SH) which are used as species-level units in the diversity estimates or ecological analyses (Kõljalg et al. 2013). At the 1.5% threshold, 73,929 SHs are available while at 0.5% level the number of SHs reaches 122,202 (https://unite.ut.ee/statistics.php). Beside the quality issues known to occur with public DNA sequences (Nilsson et al. 2012, 2017), most of them lack scientific names. The number of the named fungal species in GenBank was 34,878 of 25 November 2016, while there were 94,059 species-level OTUs with no species names at that time (Hawksworth and Lücking 2017). In the time of broad

usage of DNA sequencing technologies, the number of public DNA sequences without names is constantly growing (Ryberg et al. 2009). This lack of a name negatively affects sequence reusability and hampers communication in science as well as policy making. Studying herbarium specimens and using the DNA sequences from them to name the unidentified sequences remains an important strategy to reduce the number of the "dark taxa" (Schoch et al. 2014, Page 2016, Ryberg and Nilsson 2018).

Is every fungus found everywhere?

Understanding the variation in species' global distribution patterns has fascinated researchers for over two centuries (Bonpland and Humboldt 1805, Wallace 1876). Currently, robust biogeoregionalization frameworks are available for animals and plants (Takhtajan 1978, Kreft and Jetz 2010, Linder et al. 2012, Holt et al. 2013). Fungal biogeography remains less explored (Mueller et al. 2007, Lumbsch et al. 2008). In addition to the problems of recording and communicating the taxa of fungi, one false assumption hampered studying their broad-scale diversity patterns. Most fungi disperse by microscopic windborne spores that can travel across continents. Consequently, scientist in the past suggested that fungal species have cosmopolitan distributions and are not limited by biogeographical contingencies (e.g. Moncalvo and Buchanan 2008, Sato et al. 2012). It is now widely accepted that this is not the case (Peay et al. 2010, Tedersoo et al. 2014, Hattori 2017). Even if fungal spores can disperse long distances by air current, the probability of effective dispersal decreases very rapidly with distance, meaning that fungi can be dispersal-limited even at the small spatial scales (Galante et al. 2011, Norros et al. 2014).

A recent study of soil fungi identified climate, edaphic conditions and distance from the Equator to be the best predictors for explaining soil fungal richness and community composition at global scale (Tedersoo et al. 2014). As animals and plants, soil fungi follow the general biogeographical principles of Tropical Conservatism Hypothesis which postulates that older phyla are more prevalent around Equator, and Rapoport's Rule, which states that average distribution ranges are broader towards poles and that endemicity is most pronounced in tropics (Tedersoo et al. 2014, Treseder et al. 2014). According to these recent studies, most soil fungi follow Wallace's biogeographic rule which theorizes decreasing species richness with increasing distance from Equator. However, ectomycorrhizal fungi have a peak of species richness in the temperate zone, explained by their tight associations to *Pinaceae* host trees (Tedersoo et al. 2014, Shiryaev 2014). Though these revolutionary studies have provided valuable novel insights on fungal biogeography, many basic macroecological aspects remain unresolved. These studies focused on the soil fungi, whose function is often unknown, and other important functional guilds of fungi acting above-ground remain unexplored. Importantly, while encompassing global spatial scales (Tedersoo et al. 2014, Davison et al. 2015), these studies have little regional resolution, and thus we still lack of regional biogeographical patterns.

Why study aphyllophoroid fungi?

This study focuses on the diversity of aphyllophoroid fungi. These fungi form neither an evolutionary nor an ecological group but are often targeted as a research object because of both strong taxonomic tradition and sampling convenience. During most of the 20th

century, fungi with macroscopic fruitbodies were taxonomically classified according to their fruitbody morphologies. Several generations of mycologists were trained using the morphological classification of fungi. Though these morphological groups barely represent monophyletic taxa and are usually the result of convergent evolution (Hibbett 2007), the present-day identification keys for macrofungi for practical reasons are still compiled based on the principal fruitbody type (Krieglsteiner and Kaiser 2000, Bernicchia and Gorjón 2010, Ryvarden and Melo 2014).

Aphyllophoroid fungi represent those macrofungi from the phylum Basidiomycota R.T.Moore which do not develop gills or closed reproductive structures but have smooth, toothed, irregularly folded to poroid hymenophore and one-celled basidia. They were previously treated as a single taxonomic order but are now found among ca. 20 orders mostly of the class Agaricomycetes Doweld (Kirk et al. 2008, Hibbett et al. 2014). They comprise a highly diverse group both in terms of species richness and functional differentiation. They are the most important agents of wood decay globally (Stokland et al. 2012), but also include mycorrhizal species, plant pathogens and litter saprotrophs (Tedersoo and Smith 2013). In general, aphyllophoroid fungi are strongly dependent on woody plants in terms of nutrition and habitat.

The depth of knowledge about diversity of aphyllophoroid fungi differs between the regions of the world. For example, fruitbody-based species occurrences are more abundantly recorded in the temperate regions than in the tropics. The most straightforward reason of such difference is the lack of scientific names and taxonomic literature for the tropical fungi. Therefore, while there is a potential to analyse the diversity patterns of fungi from the temperate areas, the primary task of the tropical mycology is to provide the species names, keys and occurrence data for the new taxa. In this study, we compile and analyse the dataset of aphyllophoroid fungi in Europe to infer their diversity patterns in this best explored temperate region (papers I and IV). On the other hand, we contribute to the knowledge of tropical fungi by describing new species and revising existing species concepts in genera *Subulicystidium* Parmasto and *Trechispora* P. Karst. (papers II and III).

In Europe, diversity of aphyllophoroid fungi is documented better than on any other continent. Up-to-date taxonomic treatises and identification keys to these fungi at the continental scale are available (Bernicchia and Gorjón 2010, Ryvarden and Melo 2014). From the currently described ca. 3,000 species worldwide, a half of them has been considered to occur in Europe (Mueller et al. 2007). Nevertheless, even in Europe, along with successful projects and web platforms managing fungal diversity data (Abarenkov et al. 2010, Andrew et al. 2017), there is a plenty of records to be digitized and made open and reusable (I, IV). There are also still many regions and habitats to survey for the sake of data completeness at spatial and temporal scales (Dahlberg et al. 2010).

Despite some regional efforts, mainly in boreal Fennoscandia (Kotiranta et al. 2009, Nordén et al. 2013), Caucasus (Ghobad-Nejhad et al. 2012) and in the beech distribution area of temperate Europe (Heilmann-Clausen et al. 2014, Abrego et al. 2015, 2017) knowledge of aphyllophoroid fungal diversity patterns in Europe is limited. The close associations to live or dead plants in many species suggest that vegetation types greatly influence community composition, but it remains unknown to which degree vegetation zones structure aphyllophoroid fungal communities. A better understanding of how fungal communities depend on their host communities provides the possibility to gain insights into co-evolutionary relationships between fungi and plants (Heilmann-Clausen et al. 2016) and

how biogeographical legacies affect current distribution and host-specifity patterns (Auger-Rozenberg et al. 2015, Triponez et al. 2015).

In Europe, there is no general congruency among taxonomic groups regarding spatial diversity gradients (Keil et al. 2012). In spermatophyte plants, liverworts and several animal groups, nestedness increases towards the North as a result of the delay in post-glacial recolonization, whereas species turnover increases towards the South, as a response to the lower impact of the last glacial maximum and higher environmental heterogeneity (Hortal et al. 2011, Svenning et al. 2011). Among bryophytes, liverworts follow the same patterns as spermatophyte plants, whereas mosses follow an inverse pattern, with higher nestedness in the South due to exclusion of drought-intolerant species (Mateo et al. 2016). Given previous knowledge about host-tree specificity of many aphyllophoroid fungi, our working hypothesis was that plant-based biogeographical regions largely determine the distributions and diversity of European aphyllophoroid fungi. Further, we expected species richness to decrease and nestedness to increase towards the north, reflecting decreasing diversity in host-plant species (IV).

While conducting a survey of tropical fungi within a LOEWE-funded project of Integrative Fungal Research (IPF, http://www.integrative-pilzforschung.de), we collected specimens belonging to the genera *Subulicystidium* and *Trechispora* that could not be attributed to an any know species. Both genera belong to the family Hydnodontaceae Jülich of the order Trechisporales K.H.Larss. (Larsson 2007). The two genera have a lot in common in terms of knowledge on species diversity and distribution, which remain largely unexplored.

The genus *Trechispora* was established by Karsten (1890) to accommodate species with soft resupinate fruitbodies, poroid hymenophore and aculeate spores. *Trechispora* currently comprises 46 species (Kirk et al. 2008). Most of the accepted names were introduced by (Liberta 1966, 1973) and Larsson (1994, 1995, 1996) Larsson. After that few species have been added (Ryvarden 2002, Trichiès and Schultheis 2002, Miettinen et al. 2006). From the 46 *Trechispora* species listed in the Dictionary of Fungi (Kirk et al. 2008), 37 species are described based on collections from boreal and northern temperate zones. Therefore studies going beyond these biomes accumulate numerous specimens insufficiently identified as "*Trechispora sp.*" (Telleria et al. 2013). In addition, the DNA barcode region is sequenced only for a small portion of described *Trechispora* species. A poor knowledge on tropical and subtropical *Trechispora* species, however, does not mean that they are rare. On the contrary, they seem to be abundant throughout the world (Larsson 1992).

The genus *Subulicystidium* was created by Parmasto (1968) to accommodate corticioid fungi with long subulate or sword-like cystidia with a unique encrustation. Currently, nine species are recognized based on morphological features (Index Fungorum, 2018). Species delimitation in *Subulicystidium* has remained challenging. Basidiospore size and shape were traditionally used as the main discriminating characters, while other microscopic structures of fruit bodies were considered as generally invariable (Oberwinkler 1977, Boidin and Gilles 1988, Duhem and Michel 2001). Despite the general progress in molecular identification of fungi during the last three decades (Kõljalg et al. 2013), almost no data on the genetic diversity within *Subulicystidium* has been published and the genus remains poorly represented in all kinds of molecular studies. Currently available public sequences are usually identified to genus level only, or even just named "Trechisporales". Public sequences from fungal fruitbodies annotated to the species level are few (Volobuev 2016).

Originally, we attempted to identify *Trechispora* and *Subulicystidium* specimens from Réunion Island (Indian Ocean), which was one of the key sampling areas in the IPF project. To make this possible, specimens loaned from other herbaria sampled in numerous localities of Paleo- and Neotropics were subsequently involved in the study. This helped to provide a broader look onto diversity and distribution of these fungi, when applying morphological and DNA-based methods to explore their species boundaries (II, III).

AIMS

The overall aim of this thesis is to fill in gaps in occurrence data and taxonomy and in understanding of spatial diversity patterns of aphyllophoroid fungi. The specific aims of the study are:

- To digitize and make openly accessible the records of aphyllophoroid fungi from Europe and several tropical areas according to the current standards of publishing biodiversity information (I–IV).

- To describe the new species in the genera *Trechispora* and *Subulicystidium* and provide reference DNA sequence data and morphological key for their identification (II, III).

- To evaluate the variability of fungal DNA barcode region in a single genus *Subulicystidium* upon a comprehensive taxon sampling (III).

- To describe the spatial diversity patterns of aphyllophoroid fungi in Europe and to identify the factors shaping these patterns (IV).

MATERIALS AND METHODS

Data sampling

Specimens

Studied herbarium specimens represent fungal fruitbodies which were sampled in a living condition according to the standards for collecting macrofungi (Lodge et al. 2004). Noticeable specimens collected by us were photographed directly in the field or after drying in the laboratory. Specimens were dried with an electric fan dryer on the day of collection and placed in grip seal plastic bags. Shortly after drying, the specimens were placed into a deep freezer (-20°C) for a week, to prevent their destruction by insects.

Study I dealt with specimens of aphyllophoroid fungi collected in eastern Ukraine between 2007 and 2011 in the course of master project of Alexander Ordynets. These specimens are kept in the V.N. Karazin National University Herbarium, Kharkiv, Ukraine (CWU) and mycological collection of the University of Tartu TU (M). Study II considered specimens of *Trechispora* from Réunion Island (preserved in KAS—University of Kassel, Germany, and FR — Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany) and Papua New Guinea (TU). In the study III, herbarium specimens of *Subulicystidium* collected in several regions of Paleotropics (Réunion Island, Madagascar, Africa, South-East Asia) and Neotropics (Caribbean region, various countries of South America) were examined. This material was sampled during the last six decades, and preserved in the following herbaria: O (Natural History Museum, Oslo University, Norway), GB (Gothenburg University, Sweden), MG (Museu Paraense Emílio Goeldi, Belém, Brasil), SP (Instituto de Botânica, São Paulo, Brasil), LY (University of Lyon, France), FR and KAS. Study III also involved the holotype specimens of *Subulicystidium meridense* Oberw. (TUB, Tübingen University, Germany), *S. nikau* (G. Cunn.) Jülich (PDD, New Zealand Fungal Herbarium, Landcare Research, Auckland) and the collection of *S. allantosporum* Boidin and Gilles ad interim (Boidin and Gilles 1988) from LY.

Sequences

Throughout the study, we focused on the two markers representing nuclear ribosomal DNA: internal transcribed spacer (ITS) and ribosomal large subunit-coding DNA (28S). We generated most of the sequences in the studies I–III by ourselves. When we required additional public DNA sequences, they were downloaded from the GenBank (Benson et al. 2013) and UNITE (Kõljalg et al. 2013) databases.

Observations

If the species could be readily identified in the field, the occurrence could have been recorded and published without collecting a specimen, i.e. as observation. In this way we could generate 691 observations in the study I, and they also became a part of the input data for eastern Ukraine in the study IV. Additionally, 16 observations from the land of Hesse, Germany, contributed to the species list of this area in the study IV.

Public occurrence data

Biogeographic studies often involve data recorded by other researchers and institutions. For the study IV, we used the approach described by Hortal (2008) as "aggregating survey

records", which assumes assembling local checklists from sites of known limits and areas of varying size. We assembled species lists of fungi from 39 European areas including adjacent southern geographic areas (Palestine and the south-east coast of the Caspian Sea) and Subarctic to Arctic islands (Greenland, Faroe Islands, Iceland, Svalbard). We and other authors of the study IV provided species lists for 16 areas, and the rest were obtained from literature or web sources. All species names were standardized according to the database Index Fungorum (2018).

Environmental data

In the study IV, areas were assigned either to northern or southern Europe based on geographical latitude of 50° as a threshold. Apart from the classification of each of the areas into biogeographical regions following European Environmental Agency (EAA 2015), we obtained data on several variables potentially driving species composition using QGis 2.10 software (http://www.qgis.org/). We pooled all environmental data for administrative units, and used average values per area in ecological analyses. Climatic data was extracted from the WorldClim 1.4 database (Hijmans et al. 2005). We selected climatic variables which were not strongly correlated (Pearson's $r<0.7$), and so retained annual mean temperature (BIO1), total precipitation (BIO12), seasonal variation of these two parameters (BIO4 and BIO15, respectively) and mean temperature of the wettest quarter (BIO8).

The distribution data of the 15 most common European tree genera/species (taxonomic resolution varied in the original dataset) were obtained from Brus et al. (2012) and transformed to the relative occupancies of each tree taxon (IV). We used the Human Footprint score (mean value for area) as an integrated measure of land-use intensity (Sanderson et al. 2002, WCS & CIESIN 2005). Finally, we calculated topographic variables of area size, perimeter, mean altitude, as well as geographic coordinates of the areas' centroids.

Morphological study

In the studies II and III, fruitbody sections from dried herbarium specimens were examined in 3% aqueous solution of potassium hydroxyde (KOH) mixed with 1% aqueous solution of Phloxine, using 100× immersion oil lens of Leica DM500 light microscope. Images were captured with built-in ICC 50 HD Camera using Leica Application Suite EZ V.3.2.1 software (Leica Microsystems Ltd., Switzerland). Measurements were done with the software "Makroaufmaßprogramm" from Jens Rüdig (https://ruedig.de/tmp/messprogramm.htm). At least 10 basidia and cystidia were measured per specimen, and their size variation was presented as the range between minimum and maximum values for the pooled measurements of all collections belonging to one species. Encrustation patterns were always described as seen under the light microscope.

At least 30 basidiospores were measured per specimen. In the study III, for a more comprehensive assessment of the spore size variation, the raw spore measurements were first subjected to outlier tests of Verma and Quiroz-Ruiz (2006), David et al. (1954) and Grubbs (1950) implemented in the "Smaff" software (Wilk 2012). Upon detecting, outliers were excluded from the sample as recommended by Wilk (2012) and in this form provided in the online Supplementary file 2 to the study III.

These filtered spore measurements were used to calculate spore size range of the species. The main range was presented as the interval into which 90% of non-outlier measurements fall, while 5% of smallest and 5% largest non-outlier measurements were included in parentheses. Calculations were done in R version 3.3.3 (R Core Team 2017). For species with at least three sequenced specimens, hypothetical intervals were calculated within which 90% of all existing individuals' specimen mean values lie based on the 90% probability level (Parmasto and Parmasto 1987). For this procedure, the method of Howe (1969) was used as implemented in the "normtol.int" function of the "tolerance" R package version 1.3.0 (Young 2010).

Molecular laboratory work

DNA was always obtained from dried fungal herbarium specimens. Total DNA was isolated according to the protocol of Izumitsu et al. (2012). Primer pairs used to amplify the complete ITS region were ITS1F/ITS4, ITS1/ITS4 and ITS1/ALR0 (White et al. 1990, Gardes and Bruns 1993, Collopy et al. 2001). The D1–D2 domains at the 5′ end of 28S were amplified with primer pairs NL1/NL4 (O'Donnell 1992) and less frequently with LR0R/LR5 (Hopple and Vilgalys 1999).

PCRs of the *Trechispora* and *Subulicystidium* collections from Réunion Island were performed with the QIAGEN kit utilising Taq DNA polymerase (II). PCRs of the remaining *Subulicystidium* collections were performed with the BIOLINE kit utilising Mango-Taq DNA polymerase (III). Amplifications were performed in 96-well TGradient Thermocycler (Biometra, Göttingen, Germany). PCR with primer pairs ITS1F/ITS4, ITS1/ALRO and NL1/NL4 was set as initial denaturation at 94°C for 3 min followed by 29 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 45 s and extension at 72°C for 60 s; final elongation was done at 72°C for 7 min. In the protocol (II), PCR with primer pair LR0R/LR5 was performed with annealing temperature 52 °C while in (III) at 48°C.

PCR products were checked on 1% agarose gel stained with GelRed fluorescence dye (BIOTIUM, Hayward, CA, USA) in the Transilluminator Biometra Ti5 equipped with BioDocAnalyze software (Biometra GmbH, Göttingen, Germany). PCR products were cleaned with QIAquick PCR Purification Kit according to manufacturer's instructions (QIAGEN GmbH, Hilden, Germany). Sanger sequencing of purified products was performed in the facilities of the Senckenberg Research Institute and Natural History Museum (Frankfurt am Main, Germany), and by company GATC Biotech AG (Constance, Germany). The primers used for sequencing were identical to those used for amplification.

DNA sequence-based analyses

Raw sequence data were processed with the software Geneious version 5.6.7 (http://www.geneious.com, Kearse et al. 2012). For various sequence format conversions and alignments viewing, Mesquite version 3.40 (Maddison and Maddison 2018), AliView version 1.19 (Larsson 2014) and Seaview version 4 (Gouy et al. 2010) were used.

Sequences from each locus, ITS and 28S, were aligned online with MAFFT version 7 (Katoh et al. 2017), with L-INS-i algorithm and other settings as default. All phylogenetic analyses were performed using GTR+G evolutionary model. For Bayesian inference of phylogeny, MrBayes 3.2.3 (Ronquist et al. 2012) was used. Maximum likelihood analyses

were performed in RAxML 8.2.10 (Stamatakis 2014). Both RAxML and MrBayes were run on CIPRES Science Gateway V 3.3 (Miller et al., 2010, http://www.phylo.org). Resulting phylogenetic trees were first viewed in FigTree v. 1.4.2 (Rambaut 2014). Further visualization and annotation were done in R version 3.3.3 (R Core Team 2017) and Adobe Illustrator CS5 (Adobe Systems, San Jose, California, USA).

In the study III, morphologically outlined species were compared in terms of genetic distances estimated separately for the trimmed ITS and 28S alignments. For this, raw pairwise dissimilarities of sequences in each alignment were calculated, with the "dist.dna" function of "ape" R package where pairwise deletion option was set to "false" (Paradis et al. 2004). From these pairwise dissimilarities, intraspecific and interspecific variations were extracted and opposed to each other with the "sppDist", "maxInDist" and "nonConDist" functions of the "spider" R package (Brown et al. 2012) as recommended by Collins and Cruickshank (2012).

Ecological analyses

Study IV utilized a multi-step statistical framework which is explained in the following sections.

Gamma diversity and local species richness

All analyses were carried out using R version 3.3.3 (R Core Team 2017). Gamma diversity (i.e. the total species richness) of aphyllophoroid fungi in Europe was assessed in two ways: by constructing a sample-based accumulation curve (each area was considered a sample unit) and by applying several species richness estimators (Chao 2, Jacknife 1, Jacknife 2 and Bootstrap) using "speccacum" function of the "vegan" package (Oksanen et al. 2016).

We calculated the local species richness of aphyllophoroid fungi in the 39 European areas by summing their presences in each area. To study the relationship between species richness and environmental variables, we fitted generalized linear models (GLM) of the negative binomial family with log link function, using the "glm.nb" function from the "MASS" package (Venables and Ripley 2002).

Beta diversity

To evaluate differences in species composition across Europe, we applied the analytical framework of Baselga (2010), which decomposes beta diversity into the species turnover and nestedness components. For measuring beta diversity overall, we calculated multiple-site generalization of the Sørensen dissimilarity and derived from it multiple-site dissimilarity measures of turnover and nestedness (Baselga 2010), using "beta.multi" and "beta.sample" functions of the "betapart" R package (Baselga and Orme 2012). In this context, turnover is defined as the dissimilarity caused by substitution, of some species by others from one sampling unit to another, controlling for species richness differences. Nestedness is defined as a structured case of species richness difference, reaching the highest values when species in given species poor area are a perfect subset of species occurring in more species rich areas (Baselga and Leprieur 2015). To assess the variation of beta diversity across Europe, we compared multiple-site dissimilarity measures of Sørensen, turnover and nestedness between northern and southern Europe. We estimated the

significance in the differences of multiple-site beta diversity between two geographic belts of Europe using a permutation test (Collingridge 2013) based on an own R function which utilized "sample" function of the basic "base" package.

To assess pairwise differences in the species compositions between areas, we calculated Sørensen (1948) pairwise dissimilarity index, as well as its two components: pairwise dissimilarity index of Simpson (1943) which evaluates turnover, and the nestedness index developed by Baselga (2010). All three pairwise indices were calculated and automatically arranged into three symmetric matrices (hereinafter called Sørensen, turnover and nestedness matrices) with the "beta.pair" function of the "betapart" package (Baselga and Orme 2012). We further assessed whether the pairwise Sørensen, turnover and nestedness-resultant dissimilarities increase with a different rate (Pearson *r*) along the spatial distance between northern and southern Europe using permutation test (online Appendices S3.5-3.6 to the study IV).

Multivariate methods

To reduce the dimensionality of each of the three dissimilarity matrices and identify groups of areas with similar fungal assemblages, we applied an unweighted pair-group clustering method based on arithmetic averages, UPGMA (Borcard et al. 2011). We evaluated uncertainties in the resulting UPGMA dendrograms using the multiscale bootstrap procedure with the "recluster" package (Dapporto et al. 2013).

We evaluated the effects of the environmental variables separately for the Sørensen, turnover and nestedness matrices. For this, we performed constrained analysis of principal coordinates (CAP) on dissimilarity matrices using the "capscale" function of "vegan" package. To study directly the effect of the areas' biogeographical classification on the community composition, we built CAP models with single categorical variable specifying the assignment of each area to the European biogeographical regions (EAA 2015) as well as topography and land-use intensity. To disentangle the effect of biogeography on community composition, we built also alternative CAP models where the assignment to the biogeographical regions was replaced by the variables characterising climate and tree occupancies.

Data and protocols management

All data obtained in the study are accessible via relevant databases and/or as online supplementary files of the published papers.

The dataset of the study I (Ordynets et al. 2017) is hosted by PlutoF platform (http://dx.doi.org/10.15156/BIO/587471) and accessible from the latter under Attribution-NonCommercial-ShareAlike 4.0 International License (CC BY-NC-SA 4.0). The source records compiled into the dataset are available in the dedicated PlutoF project "Ordynets 2007-2011 eastern Ukraine" (https://plutof.ut.ee/#/study/view/38925). The specimen occurrence records may also be viewed in the GBIF occurrence dataset of CWU herbarium, Kharkiv, Ukraine (Savchenko 2017, https://doi.org/10.15468/kuspj6). All data resources are also provided in online supplementary material 1 of the study I (https://doi.org/10.3897/BDJ.5.e22426.suppl1).

For the study IV, among others, fungal species lists from three large areas were used. For the area of eastern Ukraine, the dataset of Ordynets et al. (2017) was a source of data.

For Ukrainian Carpathians, specimens from PlutoF project "Ordynets Ukraine Transcarpathia" (https://plutof.ut.ee/#/study/view/20827) were utilised. For the land of Hesse (Germany), using largely the list of Langer (2000), we could add additional occurrences based on specimens and observations recorded by Alexander Ordynets between 2013 and 2017. They can be accessed under the PlutoF project "Ordynets_Central Europe" (https://plutof.ut.ee/#/study/view/24496). For the study IV in a whole, species presence-absence data, full list of data sources as well as descriptions of the areas are provided in the online supporting information to the paper (see online version of the paper at https://onlinelibrary.wiley.com/doi/full/10.1111/jbi.13203).

Species observations used in the studies I and IV are also accessible via pooled PlutoF observations dataset (PlutoF 2017, https://doi.org/10.15156/bio/587440).

Field data and photos of recent collections from Réunion Island stored in FR and KAS herbaria (II, III) are accessible via PlutoF project "Ordynets_Fungi of Reunion Island" (https://plutof.ut.ee/#/study/view/26945) and as a part of GBIF occurrence dataset of the Senckenberg herbarium FR (Senckenberg... 2018, https://doi.org/10.15468/0oaq5v). In the study III, Supplementary file 1 contains collecting information on all 144 specimens examined, including the results of data mining from the web when the original information was not complete.

DNA sequences generated for the study II were deposited in the UNITE database (Kõljalg et al. 2013) and their accession numbers are available in the Table 1 of the paper II. DNA sequences obtained in the study III are available in the GenBank (Benson et al. 2013) under accession numbers MH041511-MH041559 for ITS and MH041560-MH041610 for 28S region. Furthermore, in the study III, the multiple sequence alignments, details of phylogenetic analyses and trees generated in the study were deposited in TreeBASE: http://purl.org/phylo/treebase/phylows/study/TB2:S22473.

In the study III, morphological data were proceeded according to the protocols deposited at https://www.protocols.io and published by Ordynets and Denecke (2018) and (Ordynets 2018b). DNA sequences were analysed with the protocols of Ordynets (2018a) and (Ordynets 2018c), and phylogenetic tree visualizations done according to Ordynets (2018d).

RESULTS AND DISCUSSION

New species occurrence data (I–IV)

As each of the studies I–IV had a specific aim, they differed in the amount and type of biodiversity information generated and used (see Table 1 for summary). In general, number of species considered in a study varied between 18 (II) and 1,491 (IV).

Study I considered 2,727 specimens of aphyllophoroid fungi from eastern Ukraine. Study II considered eight specimens of *Trechispora* from Réunion and Papua New Guinea (TU). In the study III, 144 herbarium specimens of the genus *Subulicystidium* were examined. One hundred twenty-three specimens from the PlutoF project "Ordynets_Central Europe" (https://plutof.ut.ee/#/study/view/24496) originate from Hesse, Germany, and were used to compile the species list of this area in the study IV. In the same way, 332 specimens from the PlutoF project "Ordynets Ukraine Transcarpathia" (https://plutof.ut.ee/#/study/view/20827) contributed to the species list of Carpathians in the study IV.

Study I included 691 species observations from eastern Ukraine, which were also used in the study IV together with additional 16 observations from Hesse, Germany. In total, study IV considered 14,030 species occurrence facts. This number means counts of species presence facts and thus is lower than the number of raw species occurrence records checked when compiling species presence-absence matrix.

In the study I, we generated 19 ITS sequences and four 28S sequences and additionally used seven ITS and two 28S sequences from other studies (Table 1). In the study II, we generated six ITS sequences and four 28S sequences and used further public 21 sequence of ITS and 17 sequences of 28S for molecular analyses of *Trechispora*. In the study III, we obtained 49 sequences of ITS rDNA and 51 sequences of 28S rDNA region from *Subulicystidium* specimens. Additional ten ITS and six 28S public sequences of *Subulicystidium* and two ITS and two 28S sequences of *Brevicellicium* K.H. Larss. & Hjortstam were included in the molecular analyses.

Table 1. Usage of different types of biodiversity information in the study

Study	Occurrence record type				Number of nuclear ribosomal DNA sequences			
					Newly obtained		Downloaded from databases	
	Species	Specimens	Observations	Public records	ITS	28S	ITS	28S
I	349	2,727	691	–	19	4	7	2
II	18	8	–	–	6	4	21	17
III	18	144	–		49	51	12	8
IV	1,491	455	16	14,030*	–	–	–	–

* This number accounts for the species reported as specimens and/or observations in the study I as well as for records from Hesse, Germany, and Ukrainian Carpathians

In the study I, 287 photographs depicting diagnostic macro- and microscopic features of fungal fruitbodies as well as studied habitats were linked to the dataset. They can be viewed as files associated with specimens or study areas under the PlutoF project "Ordynets 2007-2011 eastern Ukraine" (https://plutof.ut.ee/#/study/view/38925). Among such linked files are our photographs of *Dichomitus squalens* (P. Karst.) D.A. Reid (specimen CWU 6509, see web page https://plutof.ut.ee/#/specimen/view/1170949) and *Lenzites warnieri* Durieu & Mont. (CWU 6505, see web page https://plutof.ut.ee/#/specimen/view/1170945) which illustrate the respective species in the latest key to European poroid fungi (Ryvarden and Melo 2014).

Two new *Trechispora* species with peculiar morphological and ecological traits (II)

In the study II, two new species of *Trechispora* were described: *T. cyatheae* Ordynets, Langer & K.H.Larss. and *T. echinocristallina* Ordynets, Langer & K.H.Larss. Both species were repeatedly collected in 2013 and 2015 in tropical rain forests of Réunion Island (West Indian Ocean). In addition to Réunion, we reported *T. echinocristallina* from Papua New Guinea. Maximum likelihood and Bayesian inference of phylogeny based on rDNA concatenated ITS and LSU dataset confirmed that two new species belong to *Trechispora* and are distinct from all currently sequenced species of this genus (II).

Trechispora cyatheae has very small basidiospores not exceeding 3.5 µm length. The species was hitherto found exclusively on dead frond stipes of the tree fern *Cyathea glauca* which is endemic to Réunion. Up to now there is no records from two other *Cyathea* species also found on island (*C. borbonica* Desv. and *C. excelsa* Sw.) but occurring all over Mascarene archipelago (Grangaud 2010). Future observations on Réunion are needed to verify whether it is a case of narrow ecological specialization.

Trechispora echinocristallina has unique crystal aggregations composed of thick-walled crystalline spheres, covered by numerous radially protruding needle-like crystals. This crystal configuration was hitherto not known in Trechisporales. Species *T. echinocristallina* has thick dimitic fruitbodies (with skeletal hyphae) but in phylogenetic analyses was recovered nested among several monomitic species (having no skeletal but only generative hyphae). Therefore, we provided here the first molecular confirmation for keeping dimitic *Trechispora* species together with monomitic ones. *Trechispora echinocristallina* was found on tiny woody and non-woody forest debris and soil. It demonstrates well a non-true wood-decaying habit of *Trechispora* that was noted by Larsson (1992). A number of ITS sequences of *Trechispora* from soil are currently known (Högberg et al. 2014). As indigenous ectomycorrhizal host trees are missing on Réunion (Triolo 2014), it may indicate a saprotrophic lifestyle for *T. echinocristallina.*

***Subulicystidium*: twice more species than known before (III)**

In study III, we described 11 new species of *Subulicystidium* based on morphological evidence and rDNA ITS and 28S sequence analyses. The new species are:

- *Subulicystidium boidinii* Ordynets, M.M.Striegel & Langer
- *S. fusisporum* Ordynets & K.H.Larss.

- *S. grandisporum* Ordynets & K.H.Larss.
- *S. harpagum* Ordynets, M.M.Striegel & K.H.Larss.
- *S. inornatum* Ordynets & K.H.Larss.
- *S. oberwinkleri* Ordynets, Riebesehl & K.H. Larss.
- *S. parvisporum* Ordynets & Langer
- *S. rarocrystallinum* Ordynets & K.H.Larss.
- *S. robustius* K.H.Larss. & Ordynets
- *S. ryvardenii* Ordynets & K.H.Larss.
- *S. tedersooi* Ordynets, Scherf & Langer

Ten of these new species are characterized by a unique combination of basidiospore and cystidium morphology, and rDNA sequence identity. Only in one species (*S. ryvardenii*) DNA could not be amplified but the morphological evidence itself was sufficient for describing it as a new species. Morphological and DNA-evidenced borders were revised for the five previously known species: *S. naviculatum* Oberw., *S. nikau* (G.Cunn.) Jülich, *S. obtusisporum* Duhem & H.Michel, *S. brachysporum* (P.H.B.Talbot & V.C.Green) Jülich and *S. meridense* Oberw.

We estimated species-level variation in basidiospore size and shape based on systematic measurements of 2840 spores from 67 sequenced specimens of *Subulicystidium*. We defined three groups of species according to the principal basidiospore shape: species with fusiform, cylindric and allantoid basidiospores. We found that some of the species could be delimited based on the basidiospore morphology solely, while for other species this was not possible and additional morphological characters had to be considered.

The species with fusiform basidiospores were barely distinguishable according to the basidiospore length. It varied generally from 8 to 11 µm, while the mean value did not exceed 10 µm. The only exception was *S. fusisporum* which had spores 10.7–12.3 µm long (main range, i.e. 5–95% quantiles of measurements data) and 11.5 µm long in average. However, spore width and length to width ratio were useful to discriminate the species *S. naviculatum, S. ryvardenii* and *S. tedersooi*. Two species, viz. *S. robustius* and *S. inornatum* were indistinguishable in the spore width (2.5–3.5 µm) but each had peculiar cystidia.

Among the species with allantoid (i.e. reniform or phaseoliform) spores, *S. oberwinkleri* had distinctly the largest spores (mean length and width 9.2 and 4.7 µm, respectively). *S. nikau* could be distinguished from *S. boidinii* by broader spores (mean width 4.2 µm vs. 3.1 µm). Two species, *S. harpagum* and *S. parvisporum*, had rather overlapping spore width and length to width ratio but differed in the spore length: 5.6–8.3 µm (mean 6.7 µm) in the former versus 5.0–6.2 µm (mean 5.6 µm) in the latter.

Species with cylindric basidiospores were well distinguished by the mean spore length: 12.7 µm in *S. grandisporum*, 10.7 µm in *S. obtusisporum* and 9.2 µm in *S. rarocrystallinum*. The collections of the meridense-brachysporum morphogroup had shorter spores and were less clearly distinguishable.

Phylogenetic trees built with Bayesian and Maximum likelihood algorithms for ITS and 28S dataset showed a concordant pattern of species relationship. Monophyletic and polyphyletic taxa as well as several species represented by a single sequence could be found. Species with the holotype from Réunion, viz. *S. parvisporum, S. harpagum* and *S. boidinii*, were recovered as sister taxa. *S. robustius* was recovered as a distinct clade from Neotropics

subtended by a long branch. *S. fusisporum* from Caribbean region is a sister species to *S. tedersooi* from Vietnam.

With our contribution, the number of the known species in the genus *Subulicystidium* now totals 20. With account to the newly obtained data, we provided the key to the genus *Subulicystidium* (III).

Subulicystidium brachysporum and *S. meridense* are polyphyletic (III)

In the study III, we found that, despite differences in the protologues, morphospecies *S. brachysporum* and *S. meridense* are hard to separate morphologically. Analysing numerous rDNA sequences from different localities showed that currently molecular basis for delimitation of these two species is also weak.

Reviewing taxonomic literature on *Subulicystidium* brought us to delineating two morphogroups in the species *S. brachysporum*, according to the views of the earlier authors. Talbot (1958), while describing *Peniophora longispora* var. *brachyspora*, characterized its basidiospores as "elliptic-fusoid, 6.4–8 × 2.2–3.2 µm … sometimes with a faint band about the middle". Boidin and Gilles (1988) described the basidiospores of *S. brachysporum* from Réunion as elliptic in frontal face and bananiform (cylindric with slightly attenuated apex, slightly curved) in lateral face, 7.5–10 × 2–2.5(–3) µm. Therefore, we differentiated groups of (i) *S. brachysporum* sensu Talbot, i.e. sensu typi, with straight oblong-elliptic basidiospores having long attenuated base, with the mean length below 7.5 µm and mean length to width ratio hardly reaching 3; and (ii) *S. brachysporum* sensu Boidin and Gilles with cylindric and slightly curved basidiospores with the mean length over 7.5 µm and length to width ratio between 3 and 4. When describing *S. meridense*, Oberwinkler (1977) stressed the importance of allantoid, i.e. clearly curved, basidiospores. We adhered to this concept assigning our collections to *S. meridense*. We named those with similar spore size but with straight cylindric spores "*Subulicystidium* aff. *meridense*".

Morphological comparison showed that *S. brachysporum* sensu Boidin and Gilles (1988) had in average slightly longer basidiospores than *S. brachysporum* sensu Talbot (1958), viz. 7.9 µm versus 7.3 µm. Curved spores of the classical *S. meridense* were in average shorter than straight spores of *S.* aff. *meridense*, viz. 6.9 µm versus 8.2 µm. Spores in the type specimen of *S. meridense* were of the intermediate average length compared to the two former examples (7.4 µm). The spore width and length to width ratio were very much overlapping in the material of meridense-brachysporum morphogroup.

Four morphological groups, two within *S. brachysporum* and two within *S. meridense*, were not recovered as distinct using DNA sequence similarity analyses and phylogenetic reconstructions. All sequences of *S. brachysporum* and *S. meridense* with their likes were found in four clades of ITS- and 28S-based phylogenetic trees. One such clade contained also single sequences of *S. obtusisporum* from Germany and *S. harpagum* from Jamaica. Second clade included more collections of *S. brachysporum*, mostly sensu Boidin and Gilles (1988), and less of *S. meridense*, but also a single sequence of *S. grandisporum*. Third large clade was roughly equally rich on sequences of *S. brachysporum* and *S. meridense* and joined by a single sequence of *S. inornatum*. One sequence of *S. brachysporum* (GB:KHL 10411) was placed in a clade, though weakly supported, with three sequences of *S.*

longisporum from Europe. Therefore, *S. brachysporum* and *S. meridense* in current understanding are highly polyphyletic.

Nuclear ribosomal DNA sequence variation in *Subulicystidium* upon a comprehensive taxon sampling (III)

To asses a variability of nrDNA in *Subulicystidium* (III), we used own sequences of the ten new species and four known species. We also used public sequences of the species *S. longisporum* and *S. perlongisporum* and included two sequences of *Brevicellicium* as an outgroup.

Aligned ITS sequences fell into several dissimilarity categories. All the *Subulicystidium* sequences were at least 10% different from two *Brevicellicium* sequences (outgroup), as well as from single sequence of *Subulicystidium oberwinkleri*. The sequences of *S. robustius* were at least 3% and maximum 10% different from the rest of the genus. The sequences of *S. harpagum* and *S. parvisporum* were most distant from *S. robustius* (7–10%) and 3-7% distant from the rest of the genus. Sequences mostly belonging to morphospecies *S. meridense* and *S. brachysporum* formed four groups within which they were all 0-3% (in many cases only up to 1%) dissimilar. One of these groups included also sequences of *S. fusisporum* and *S. tedersooi*, another group—*S. longisporum* and *S. grandisporum* and the third—single sequence of *S. obtusisporum*. Therefore, both easier and harder distinguishable species, in terms of ITS region identity, were found in the dataset.

The pattern seen through a visual inspection of the ITS sequence dissimilarity matrix was confirmed by the barcoding gap analysis. Throughout the dataset, intraspecific and interspecific distances strongly overlapped and no universal for the genus *Subulicystidium* barcoding gap could be detected. Mean and maximal intraspecific distances were 2.87 and 7.73%, while mean and minimal interspecific distances were 5.06 and 0%, respectively. At the level of individual species, barcode gap existed for *S. fusisporum*, *S. parvisporum*, *S. robustius* and *S. tedersooi*.

Pairwise 28S sequence dissimilarities were structured differently compared to the ITS dataset. The most distinct species in terms of 28S identity was *S. oberwinkleri*. The dissimilarity of its two sequences from the rest of *Subulicystidium* and two *Brevicellicium* sequences was 10-20%. The next most distinct group was formed by the sequences of *S. harpagum* and *S. parvisporum* which were 7–10% dissimilar from the rest of the genus except one group containing *S. meridense* and *S. brachysporum* sequences (2–3%). The majority of dissimilarities laid in the range 1-5% and were clearly grouped.

In a whole 28S dataset, intraspecific and interspecific distances strongly overlapped and thus showed no universal for the genus *Subulicystidium* barcode gap. Mean and maximal intraspecific distances were 2.52 and 12.5%, while mean and minimal interspecific distances were 5.58 and 0%, respectively. At the level of individual species, barcoding gap was evident for *S. oberwinkleri*, *S. fusisporum*, and *S. robustius*.

Geographical distribution of the newly introduced and revised taxa (II, III)

The type species of the genus *Subulicystidium*, *S. longisporum*, is often reported and mapped in mycodiversity surveys worldwide (e.g. see Subulicystidium…, 2017). In contrast, other species are still known either from the type locality only (*S. curvisporum*

Gorjón, Gresl. & Rajchenb.), or from a few localities: *S. cochleum* Punugu, *S. meridense* Oberw., *S. naviculatum* Oberw., *S. nikau* (G. Cunn.) Jülich and *S. obtusisporum* Duhem & H. Michel (Punugu et al. 1980, Gorjón et al. 2012). Some species records represent more than one continent but in all cases these reports are based on a morphological species concept (Boidin and Gilles 1988, Duhem and Michel 2001, Volobuev 2016).

Our study III was based on morphological examination and DNA sequencing of a large set of specimens from numerous localities in Paleo- and Neotropics. We could gain the first information on the distribution of new species. For example, *S. robustius* is in fact a frequently occurring species in the Caribbean region and in South America. On the other hand, we could report a multicontinental distribution for several species, verified by DNA sequence data. *S. brachysporum, S. boidinii, S. harpagum* and *S. oberwinkleri* are typified by material from Paleotropics (South Africa in the first species and Réunion in three others), but were found by us also in South America. The morphospecies *S. meridense,* described from Venezuela (Oberwinkler 1977) and later found in Costa Rica (Kisimova-Horovitz et al. 1997), was also found on Réunion Island by Boidin and Gilles (1988). In addition to sequenced collections from a few more countries in South America, we confirmed the species presence on Réunion by sequencing collections of Boidin and Gilles (1988). In this study, we report *S. meridense* for the first time from South-East Asia (Taiwan). The new species *S. fusisporum* was first considered by us as a Caribbean endemic. Re-identification as *S. fusisporum* of the specimen collected by G. Gilles in Côte D'ivoire (LY 7375, originally labelled as *S. longisporum,* DNA could not be amplified) may suggest that species occurs in West Africa as well.

We typified the new species *Trechispora echinocristallina* by specimen from Réunion Island. When performing BLAST similarity search of ribosomal DNA from Reunionese specimens, we found highly similar sequence from the unidentified fruitbody from Papua New Guinea (collected in 2011 and preserved in TU). After studying this collection, we confirmed its morphological identity with Réunionese material (II). Therefore, distribution of *T. echinocristallina* covers two very distant tropical localities.

It was surprising for us to find the species occurring on more than one continent or on islands separated by thousands of kilometres. For fungi with spores carried by wind, dispersal limitation was shown to act strongly even at small spatial scales (Peay et al. 2010, Norros et al. 2012). Given the architecture and location of *Subulicystidium* and *Trechispora* fruitbodies (next to the ground, not rarely underside of the logs), one would expect prevailing spore dispersal distance smaller than 1 m (Galante et al. 2011). However, in macrofungi there remains a probability of spore travel on a distance of kilometres (Nordén and Larsson 2000, Peay et al. 2012, Norros et al. 2014) and also overseas (Geml et al. 2012). Spore morphology traits have been recently discussed in a connection to dispersal and arrival success of a species (Norros et al. 2014, Calhim et al. 2018). In this regard, the genus *Subulicystidium,* with a high diversity of spore size and shape between species, is an interesting object to correlate spore traits and biogeography in future studies.

Comprehensive account of the known aphyllophoroid fungal diversity in Europe (IV)

In the study IV, we first analysed patterns of fungal alpha-diversity in relation to the plant-based biogeographical regions (EAA 2015). From the 39 European areas we

assembled 14,030 records of 1,491 fungal species. The species accumulation curve indicated a very thorough sampling of European aphyllophoroid species in our data, but richness estimators indicated the total species richness to be 142-461 species larger than observed. Our predictions of species richness were almost identical to those performed by Mueller et al. (2007), who, based on the opinion of expert taxonomists, estimated the existence of about 1,900 aphyllophoroid species in Europe. Most likely, the most underrepresented group of aphyllophoroid fungi in our dataset are species with smooth effused ephemeral fruitbodies that are often overlooked in field studies (Abrego and Salcedo 2015), and are known to encompass many cryptic species (e.g. Balasundaram et al., 2015).

Spatial variation of species richness of aphyllophoroid fungi in Europe (IV)

Among the plant-based biogeographical regions, the Arctic region held the least species (52.6 on average) while the Alpine, Atlantic, Boreal and Continental biogeographical regions all harboured at least 200 species (404.9 on average) with no significant differences among regions. However, there was a clear trend of decreasing species richness towards the southern biogeographical regions (Mediterranean — 291.5 species, Steppic — 296.5 species, and Hyrcania — 304.0 species).

Since many aphyllophoroid fungi are associated with dead wood, their lowest species richness in the Arctic was not surprising. The diversity of woody hosts and amounts of dead wood are very limited in Arctic areas. Results from recent studies suggest that aphyllophoroid fungal communities in Arctic areas are to a large extent explained by arrival of pre-colonized driftwood which originates from non-Arctic parts of Europe, Asia and North America (Rämä et al. 2014, Ryvarden 2015). Interestingly, we also found a trend of decreasing species richness and increasing turnover towards southern areas (Mediterranean, Steppic biogeoregions and south-east coast of the Caspian Sea). These regions are the richest in plant species and also harbour the highest diversity of woody hosts. Studies from other continents support the finding that the highest aphyllophoroid fungal species richness is found at middle latitudes and decreases towards the north and south (Mukhin 1993, Shiryaev 2014, Gonzalez-Avila et al. 2016), indicating that aphylloporoid fungal diversity might generally be lower in warm and/or dry regions. This could reflect that the often long-lasting aphyllophoroid fruitbodies are poorly adapted to stressful climates, which typically involve strong fluctuations in humidity and extreme temperatures. Shift to insect-driven wood decomposition, which is enhanced in warmer climates (Müller et al. 2015) may be a further explanation to the lower aphyllophoroid diversity in these regions.

Spatial variation of community composition of European aphyllophoroid fungi in Europe (IV)

In the study IV, we further analysed patterns of fungal beta-diversity in relation to the plant-based biogeographical regions (EAA 2015) and in relation to the areas' location in southern versus northern Europe. The Sørensen beta diversity value for the total fungal dataset was 0.92. The turnover component of beta diversity dominated over the nestedness component (β_{SIM}=0.84 versus β_{SNE} = 0.08), resulting in the proportional contributions to the total beta diversity of 91% and 9%, respectively.

Overall Sørensen beta diversity, as well as turnover and nestedness, was higher in northern compared to southern Europe based on the original datasets. However, the multiple site dissimilarity analysis (of equal-size resampled data) revealed that the Sørensen dissimilarity and nestedness were higher in southern Europe. Nevertheless, these differences were all insignificant based on permutation tests.

Pairwise dissimilarities between 39 areas were mostly positively related to spatial distances (Pearson r between 0.254 and 0.442, $P < 0.01$). However, the strength of relationship was not different between southern and northern Europe based on permutation tests.

Both multiple-site and spatial beta diversity analyses showed that the beta-diversity gradients were similar in southern and northern Europe. Hereby our results resemble those obtained for bryophytes (in particular mosses), for which no differences in turnover and nestedness between southern and northern Europe have been detected (Mateo et al. 2016), indicating that climate and current habitat availability to be the main drivers of community composition.

We classified 39 European areas in relation to their fungal community composition. We found that aphyllophoroid fungal communities followed plant-based biogeographical regions to a large extent, but not as clearly as animal and plants (Heikinheimo et al. 2012). The clearest cluster in terms of community composition was formed by Arctic areas, most likely reflecting the low aphyllophoroid species richness in these areas. The cluster analyses also revealed that Mediterranean areas, south-east coast of the Caspian Sea in Iran and Steppic areas hold similar community composition. Mediterranean areas and SE coast of the Caspian Sea share a long history of similar climate and vegetation and represent glacial refugia for temperate European forest trees (Magri et al. 2006, Ghobad-Nejhad et al. 2012). A partly similar climate and geographical proximity of Steppic areas to Mediterranean areas and SE coast of the Caspian Sea may be a reason for their high similarity in fungal community composition. The community composition of Alpine, Atlantic, Boreal and Continental areas formed more complex cluster configurations. One of the reasons for this might be that some of the areas are located close to ecotones between biogeoregions and thus resemble the communities from neighbouring biogeoregions. For instance, the fungal composition of the Navarre (northern Spain), dominated by Atlantic beech forests, was more similar to Mediterranean areas than to other Atlantic areas. Likewise, the Continental area of Macedonia was closer to the Mediterranean biogeoregion than to other Continental areas. Another reason for the intermixing of biogeoregions might fall on the sensitivity of fungi to particular climatic conditions. For example, the Bavarian Forest, situated in area classified as Continental, held fungal community which clustered with Atlantic and Arctic areas, which might be explained by the high precipitation in this area (Bässler et al. 2010).

Different environmental drivers do matter for different diversity components (IV)

We modelled the fungal community composition and species richness of aphyllophoroid fungi in relation to biogeographical region, climate, host-tree distributions, topography and land-use intensity across Europe (IV). Our results show that the importance of biogeographical regions in determining European aphyllophoroid fungal communities varies for different diversity components. Species richness and nestedness were best explained by plant-based biogeographical regions. On the other hand, overall beta-diversity

and species turnover were driven mostly by variation in climate, and nestedness mostly by tree species occupancy.

Although tree species composition was a statistically significant driver of turnover in aphyllophoroid communities, we expected this variable to be even more influential. Many of our study species are plant-associated with prominent host-specialisations, and communities of aphyllophoroid fungi found in conifer forests differ strongly from those found in deciduous forests (Hattori 2005, Stokland et al. 2012). However, Heilmann-Clausen et al. (2016) recently found that major clades of aphyllophoroid fungi are less host-specialist than several other fungal lineages, especially in the Ascomycota, probably reflecting a much stronger signal of co-evolution with hosts. It is hence likely that host distribution patterns may have a stronger impact on the biogeography of fungi in other lineages than aphyllophoroid fungi belong to.

A negative effect of land-use intensity was evident for species richness but not for community composition, and geographical variables were rather weak predictors of both species richness and community composition. This contrasts with results from European vascular plants and animals, for which the effect of non-climatic variables such as land-use intensity and geographical distance were found to be strongest (Svenning et al. 2008, 2011, Keil et al. 2012). Therefore, our results suggest that aphyllophoroid fungal communities are less shaped by historical legacies than plant and animal communities, at least at the continental scale.

CONCLUSIONS

Comprehensive knowledge of biodiversity is a prerequisite for its long-term conservation and sustainable use. Biodiversity knowledge has numerous aspects and encompasses naming of organisms, recording their occurrences and analysing the latter on various spatial and temporal scales. Fungi play crucial roles in ecosystems and are among the species-richest organism groups on Earth. However, all aspects of their diversity remain underexplored.

In this study, we aimed to fill the gaps in occurrence data and taxonomy as well as in understanding spatial diversity patterns of aphyllophoroid fungi. We have digitized and made openly accessible records of aphyllophoroid fungi from eastern and central Europe and several tropical areas. Numerous specimen records were associated with DNA sequences (ITS and 28S) and numerous observations also with photographs depicting diagnostic features of fungal fruitbodies. The assignments to the lifestyle and fruitbody principal configuration type (morph) were provided for each species in the occurrence datasets.

To provide a possibility to identify and communicate hitherto unknown tropical fungi, we described 13 new species belonging to *Trechispora* and *Subulicystidium*, based on morphological and molecular analyses of nrDNA ITS and 28S sequences. We revised also the morphological and genetic borders of the five previously known species of *Subulicystidium*. Using DNA-based evidence, in the studied lineage (Trechisporales), we showed for the first time a possibility of species presence on more than one continent or on islands separated by thousands of kilometres.

With the two new species described, we extend the knowledge on *Trechispora* diversity in tropics and furthermore proved the importance of crystals for species delimitation in this genus. The findings of *Trechispora cyatheae* on tree fern *Cyathea glauca* demonstrate the importance of looking at unusual (non-woody) substrata while making mycological observations. We expect further new taxa of aphyllophoroid fungi from non-woody substrata on Réunion Island and in other tropical areas.

With eleven newly described species of *Subulicystidium*, we showed that species diversity in the genus is at least twice higher than previously known. On the other hand, based on analyses ITS and 28S nrDNA, we revealed a clear barcode gap for some of the species but problems to delimitate the others. This challenges DNA-based species identification as practiced through DNA barcoding and warns of underestimating the morphological information for species delimitation. Careful morphological examination combined with nrDNA barcode data and evidence from other DNA markers is needed to delimitate species in *Subulicystidium.*

The species richness of aphyllophoroid fungi is mostly explained by plant-based biogeographical regions, with Arctic and Mediterranean regions holding fewer species than the other regions. At the continental scale, aphyllophoroid fungi are less shaped by historical legacies than vascular plant and animal communities, and trends of overall beta diversity in southern and northern Europe are similar to patterns found for bryophytes.

In spite of the comprehensive dataset of European aphyllophoroid fungi we used, we still found ambiguities when trying to biogeographically classify the areas. To overcome this problem, future studies in this line of research could use data collected by a regular-grid or with a finer spatial resolution than in our study and include some of still largely

unexplored European areas (e.g. Southern and Eastern Europe). Moreover, comparing the spatial patterns of the species with different fruitbody traits, ecological strategies and phylogenetic relationships would help in gaining a more functional perspective on the diversity patterns of European aphyllophoroid fungi.

The dataset digitized and made openly accessible in study I shed new light on fungal diversity of Eastern Europe. Study IV provided an integrated overview of alpha and beta diversity patterns for European aphyllophoroid fungi, and revealed environmental drivers of these patterns. Studies II and III extended knowledge on taxonomic diversity and global distribution of aphyllophoroid fungi. Such literature is urgently needed to assist in tropical fungal inventories. Using a dataset covering nearly all *Subulicystidium* species known up to date (III), we provided a contribution towards better understanding of the ITS and 28S nrDNA variation in Fungi. Such information is crucial for the future development of the systems for automated DNA similarity-based fungal species identification.

The value of different research outcomes and views on how they should be communicated is now reconsidered by scientific community and general public (Gewin 2016). It is realized that research data, experimental methods and codes (scripts) for computer analyses are as important as research results and all contribute to the progress in particular discipline (Smith et al. 2013, McKiernan et al. 2016). All the research outcomes should be transparent and publicly available. However, they should also follow quality standards which make them easily discoverable and reusable by both humans and computers (Wilkinson et al. 2016). This should allow our society effectively address various challenges of the present and future (Bouchout Declaration 2014). We totally support this shift in views on publishing scientific outcomes. We see our contribution to the open biodiversity science by sharing all fungal occurrence records and associated information as DNA sequences and alignments, and analyses protocols. Our specimens and DNA sequences stored in a biodiversity data management platform PlutoF (https://plutof.ut.ee) are open for the alternative taxon identification, and our protocols deposited on https://www.protocols.io are most welcome for commenting and reuse.

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ERKLÄRUNG GEMÄSS § 8 ABS. 1 SATZ 2 LIT. D AB-PROMO

Hiermit versichere ich, dass ich die vorliegende Dissertation selbständig, ohne unerlaubte Hilfe Dritter angefertigt und andere als die in der Dissertation angegebenen Hilfsmittel nicht benutzt habe. Alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten oder unveröffentlichten Schriften entnommen sind, habe ich als solche kenntlich gemacht. Dritte waren an der inhaltlichen Erstellung der Dissertation nicht beteiligt; insbesondere habe ich nicht die Hilfe eines kommerziellen Promotionsberaters in Anspruch genommen. Kein Teil dieser Arbeit ist in einem anderen Promotions- oder Habilitationsverfahren durch mich verwendet worden.

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Datum Unterschrift des Doktoranden

PUBLICATIONS

I

Ordynets A, Savchenko A, Akulov A, Yurchenko E, Malysheva V, Kõljalg U, Vlasák J, Larsson K-H, Langer E (2017) Aphyllophoroid fungi in insular woodlands of eastern Ukraine. Biodiversity Data Journal 5: e22426. doi: 10.3897/BDJ.5.e22426

II

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III

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IV

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