

1 **Current knowledge of Chytridiomycota diversity in Northern Europe and future**
2 **research needs**

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16 **Abstract**

17 Chytridiomycota is the most species-rich phylum of basal lineage fungi involved in vital
18 processes in both terrestrial and aquatic ecosystems. Still, the diversity and richness of this
19 group remains cryptic. In Northern Europe, few species have been recorded despite the
20 numerous intact lake systems covering this region. Recent classifications of early diverging
21 fungal lineages differ considerably on the diversity of chytrid species and their taxonomic
22 placement. Here, we present the current knowledge of the Chytridiomycota diversity within
23 Northern Europe by using the Global Biodiversity Information Facility (GBIF) data and
24 compare how this diversity distributes across two recently proposed classification systems.
25 Furthermore, we illustrate how various sampling types are influencing the recorded
26 classification levels. Lastly, we discuss how metabarcoding has contributed to the overall
27 understanding of the Chytridiomycota diversity in revealing the “dark matter fungi”, and we
28 point out future research needs in the field of aquatic mycology in the Nordic region.

29

30 **Keywords:** Fungi, Chytridiomycota, Diversity, Freshwater, Nordic countries

31

32 **Introduction**

33 Fungi encompass one of the most diverse kingdoms of eukaryotes, with global diversity
34 estimates ranging from 2.2 to 3.8 million extant species (Hawksworth and Lücking, 2017).
35 They play fundamental ecological roles as decomposers (saprotrophs), mutualists, pathogens,
36 and parasites (Bass and Richards, 2011). Yet only ~150 000 species have been described
37 formally (<http://www.speciesfungorum.org>), of which only ~3,000 are from aquatic habitats
38 (Shearer et al., 2007). Aquatic fungi are a taxonomically and morphologically diverse group
39 that rely on aquatic habitats for the whole or parts of their life cycle (Grossart et al., 2019).
40 Freshwater and marine environments therefore represent priority targets for the recovery of
41 novel and seemingly uncultivable aquatic fungal lineages that have previously eluded detection
42 (Grossart et al., 2019, Nilsson et al., 2019, Nilsson et al., 2016, Richards et al., 2012).
43 Chytridiomycota (chytrids) comprise a significant proportion of fungi within water systems as
44 they are adapted to such habitats (Grossart et al., 2019, Wurzbacher et al., 2010). Recent
45 surveys in marine ecosystems report the dominance of Chytridiomycota among the detected
46 fungal species (Comeau et al., 2016, Hassett and Gradinger, 2016, Hassett et al., 2017,
47 Lepelletier et al., 2014, Picard, 2017). The chytrids are also rife in freshwater systems, where
48 they fuel a range of poorly understood ecological processes (Grossart et al., 2016, Wurzbacher
49 et al., 2010). The chytrids fill niches across all ecosystems, as they are found in soils, freshwater
50 and marine systems, and they are even present in highly adaptive habitats such as hydrothermal
51 vents (Grossart et al., 2019, Le Calvez et al., 2009, Richards et al., 2012). A number of the
52 newly discovered chytrid fungi occur primarily in lakes, where they are well adapted to an
53 aquatic lifestyle and act as saprotrophs (e.g., on pollen grains) and parasites on a wide range of
54 hosts (Kagami et al., 2014, Kagami et al., 2017, Sime-Ngando, 2012, Wurzbacher et al., 2014)
55 or exhibit a pathogenic life style (Longcore et al., 1999). Despite being recognized as important
56 in ecosystem functioning, both diversity and function of chytrids are underreported within most
57 studies in aquatic systems (Frenken et al., 2017), and an overview of regional diversity is sorely
58 missing. Chytrids are small in size and lack conspicuous morphological features, which makes
59 it difficult to distinguish them from protists (Sime-Ngando, 2012). In metabarcoding and
60 eDNA monitoring surveys the members of Chytridiomycota are seemingly challenging to
61 capture (Grossart et al., 2016), which might perpetuate the underreporting of this important
62 ecological group in current and future studies of aquatic ecosystems. In this mini review, we
63 demonstrate the current knowledge status of the chytrid diversity in Northern Europe (i.e.

64 Norway, Sweden, Finland, Denmark, and Iceland) and discuss this diversity within taxonomic,
65 historical and functional perspectives.

66

67 *Northern Europe and its lake history*

68 The Nordic region exhibits large gradients in lake water chemistry due to considerable differences in
69 bedrock geology, hydrology, precipitation amount, soil cover, vegetation, and air pollution (Skjelkvåle
70 et al., 2001). Quaternary glaciations and interglacial periods (i.e. 2.5 - 3 Ma) drastically and repeatedly
71 reshaped the present-day landscapes in Nordic countries, as well as the distribution of biota (Wohlfarth
72 et al., 2008). In particular, the northern regions were recolonized following glacial advances and ice
73 retreats (Kontula and Väinölä, 2001). The relatively young age of lakes and their multitude in the boreal
74 area compared to lakes in older landscapes are due to a wide range of geomorphological processes, such
75 as glacial restructuring of loose deposits and land uplift (Englund et al., 2013). Northern lakes have
76 been deglaciated for the past 15 000 years, and therefore their relative pristine nature provides a glimpse
77 into the past (Cott et al., 2016). Lakes are “active pipes” for carbon transport, transformation and storage
78 between terrestrial systems and atmosphere, and may act as sinks for organic matter between land and
79 the sea (Algesten et al., 2004, Cole et al., 2007, Tranvik et al., 2009). Based on the study of ca. 80 000
80 boreal lakes, 30-80% of the total organic carbon (TOC), that entered freshwater ecosystems, was
81 deposited in lakes (Algesten et al., 2004). According to Tranvik et al. (2009), lakes sequester large
82 amounts of carbon in their sediments and are therefore important for the global carbon cycling.

83 Aquatic fungi, in particular early diverging fungal phyla, represent a much overlooked yet central
84 ecological player in freshwater habitats. Although fungal species richness is correlated with latitudinal
85 gradients, very few chytrid species have currently been identified within the Nordic region underpinning
86 the status of these fungi as being overall “dark matter fungi” (Grossart et al., 2016). It is seemingly a
87 paradox that most records of chytrids are from terrestrial habitats, although the members of the
88 Chytridiomycota are known to play pivotal roles in lakes, which are numerous in Northern Europe.
89 Combined, there are approximately 370 000 lakes larger than one hectare across Norway, Sweden and
90 Finland covering between 10-30% of the land within southern/central areas (Nordic Council of
91 Ministers, 2010). Therefore, regional lake surveys and biodiversity monitoring, including the
92 understudied taxonomic groups, are necessary for accumulating baseline information with respect to
93 large-scale and long-term changes in lakes, as well as documenting past and present status of their
94 freshwater biodiversity and resources (Skjelkvåle et al., 2001).

95

96 *Chytrids in the mycocoop*

97 Aquatic systems contain a great variety of fungal habitats which serve as “hot spots” of novel
98 and unexplored fungal diversity (Wurzbacher et al., 2016, Wurzbacher et al., 2010). The

99 chytrid parasitism, chytridiomycosis, is an important ecological driving force in the aquatic
100 food web dynamics by altering sinking fluxes and facilitating energy and nutrient transfer
101 through the *mycoloop* (Frenken et al., 2017, Kagami et al., 2014, Rasconi et al., 2012, Rohrlack
102 et al., 2015, Sime-Ngando, 2012). The mycoloop represents a unique trophic link in the aquatic
103 food web, where nutrients from large inedible algal cells are transferred to zooplankton such
104 as *Daphnia* via the nutrient-rich zoospores of parasitic chytrids (Kagami et al., 2014, Kagami
105 et al., 2017, Grossart et al., 2016). In addition, large phytoplankton cells may be fragmented by
106 chytrid infections and become edible to zooplankton (Sime-Ngando, 2012). Chytrids may
107 facilitate the sinking of aggregated algal cells during the infection and thus contribute to the
108 element cycling in lakes (Kagami et al., 2014). The release of chytrid zoospores from
109 zoosporangia on inedible large pollen grains to zooplankton can function as another mycoloop,
110 especially in freshwater habitats with significant pollen deposition (Kagami et al., 2014,
111 Kagami et al., 2017). Although, the mycoloop is not restricted to chytrids only, and
112 involvement of other zoosporic fungi from the Aphelidiomycota and
113 Cryptomycota/Rozellomycota is known (Gleason et al., 2012a, Gleason et al., 2012b, Gleason
114 et al., 2014, Ishida et al., 2015, Naranjo-Ortiz and Gabaldón, 2019, Kagami et al., 2014), true
115 chytrids are the largest and most taxonomically diverse group involved in these processes. In
116 marine systems, chytrids are poorly represented, yet 26 species were included in the
117 classification of marine fungi due to overall interest, however, systematic under-sampling of
118 zoosporic fungi is reported within this habitat (Jones et al., 2015). These fungi are thought to
119 interplay with algal blooms of especially diatoms, however, little is known about such
120 processes (Amend et al., 2019). The mycoloop within marine systems is anticipated to govern
121 the trophic linkage to zooplankton (Kagami et al., 2014).

122

123 *Classification of chytrids*

124 The phylum Chytridiomycota belongs to the early diverging fungal lineages (James et al.,
125 2006a) and comprises morphologically diverse groups of true fungi that possess flagella in at
126 least one of their life cycle's stages and therefore are associated with wet habitats (Naranjo-
127 Ortiz and Gabaldón, 2019, Sparrow, 1960). Taxonomically, Chytridiomycota have previously
128 intertwined with the phyla Zygomycota and were thus not regarded to be monophyletic (James
129 et al., 2006b, James et al., 2000). A six-gene phylogeny of flagellated fungi still could not
130 delimit the chytrids, however, another phylum (Blastocladiomycota) within the kingdom Fungi
131 was described (James et al., 2006a, James et al., 2006b). This led to the separation between

132 flagellated fungi across several groups, as this character does not reflect common ancestry
133 (James et al., 2006b). In fact, at least four independent losses of flagellum have occurred across
134 the kingdom Fungi (James et al., 2006a). The new delimitation of Chytridiomycota was
135 underpinned in the comprehensive classification of fungi conducted by Hibbett et al. (2007),
136 in which Chytridiomycota sensu stricto was kept, separating out Blastocladiomycota and
137 Neocallimastigomycota in other phyla of flagellated fungi. Within Chytridiomycota, several
138 classification systems have been suggested (Hibbett et al., 2007, James et al., 2006b, Naranjo-
139 Ortiz and Gabaldón, 2019, Tedersoo et al., 2018, Wijayawardene et al., 2018). The term
140 “euchytrids” was introduced to the clades Chytridiales, Monoblepharidales, Neocallimastigales
141 and parts of the Spizellomycetales (James et al., 2006b). Barr (2001) identified a single class,
142 Chytridiomycetes, containing five orders. Later classifications accepted two classes,
143 Chytridiomycetes (three orders) and Monoblepharidomycetes (one order) (Hibbett et al., 2007).
144 In a large revision by Tedersoo et al. (2018) basal fungi were revised on the basis of monophyly
145 and divergence time to enhance comparability across studies and subsequent use in ecological
146 surveys. New taxonomic levels were included, and the phylum Chytridiomycota was described
147 containing nine classes comprising 10 orders (Tedersoo et al., 2018). In the notes for genera of
148 basal clades of fungi, two classes – 13 orders – 57 families and 151 genera were accepted
149 within the phylum based on the available information on basal clades (Wijayawardene et al.,
150 2018). The recent revision by Naranjo-Ortiz and Gabaldón (2019) identifies three classes,
151 namely Chytridiomycetes (seven orders), Monoblepharidomycetes (one order) and
152 Hyaloraphidiomycetes (one order), and estimates the diversity of the phylum to be
153 approximately 1000 species worldwide.

154

155 **Chytrid diversity**

156 *Chytrids around the world*

157 World distribution of recorded Chytridiomycetes sensu lato (classification according to James
158 et al. (2006b)) identifies four “hot spots” where chytrids have been detected more frequently,
159 i.e. USA, Central Europe, Australia and Japan (Fig 1A). However, the top 10 most recorded
160 species, including *Batrachochytrium dendrobatidis* (BD), constitutes 43 % of all “curated”
161 records. When material samples (i.e. samples detected through metabarcoding sequencing) are
162 included (Fig 1B), the record number of worldwide increases threefold, and the currently
163 recorded chytrid abundance in marine habitats is revealed.

164

165 *Chytrids in the Nordic countries*

166 Within the Nordic countries very few records of chytrid species have been made at local scales.
167 In Norway four entities of Chytridiomycota, where only two were reported at the species level
168 with a modest record of 45 and three, respectively, are included in the Species Map Service
169 (the Norwegian Biodiversity Information Centre, 2019) (Johnson Jr, 1976, Johnson Jr, 1977).
170 In Sweden and Finland combined, a total of three species have been recovered (SLU Swedish
171 Species Information Centre, 2019; Finnish Biodiversity Information Facility, 2019),
172 underpinning that Chytridiomycota is critically understudied within Fennoscandia (i.e.
173 Norway, Sweden and Finland). Still, it is important to note that some chytrid taxa, such as
174 *Zygorhizidium* are not found within either of the three abovementioned biodiversity centres but
175 have been recorded within Norway and Sweden (Canter, 1954, Seto et al., 2020). In fact, older
176 studies in Norway have detected several genera of chytrids such as *Phlyctochytrium* and
177 *Nowakowskiella* (Johnson Jr, 1976, Johnson Jr, 1977), and *Phlyctidium* has also been noted in
178 Finland (Karling, 1939). To date, no systematic survey of chytrid species diversity has been
179 made, and this may explain a limited record of Chytridiomycota and therefore a “weak” status
180 on chytrid taxonomy and diversity in Norway (Table 1). The terrestrial plant parasite
181 *Synchytrium anemones* is modestly recorded within all three countries. The highly virulent
182 chytrid species BD, infecting skin of amphibians, has been detected nine times in Norway
183 (Taugbøl et al., 2017) and Sweden (<https://www.artportalen.se/>) and is currently under
184 surveillance. Surprisingly, the knowledge status on chytrid ecology is stated to be “acceptable”,
185 albeit without the expected taxa diversity and their potential ecological roles. In Iceland, the
186 chytrid diversity was assessed based only on morphology (Howard and Johnson Jr, 1969,
187 Johnson Jr, 1969a, Johnson Jr, 1973). However, Johnson Jr (1973) focused on aquatic fungi in
188 general (including Oomycota and Zygomycota), found in both marine and freshwater
189 environments. Here, several chytrid species were recorded from these studies within six genera
190 (Johnson Jr and Howard, 1968). Further investigations in Iceland revealed at least six species
191 within the genus *Phlyctochytrium* (Johnson Jr, 1969b). Denmark is seemingly the Nordic
192 country with the highest chytrid diversity comprising 26 species across four orders
193 (<https://allearter.dk/>). Here, we used the Global Biodiversity Information Facility (GBIF) data
194 from the Nordic countries to illustrate current knowledge of chytrid diversity in this region and
195 compare the output within the two taxonomic classification systems by Naranjo-Ortiz and
196 Gabaldón (2019) and Tedersoo et al. (2018). This review focuses on chytrid species in the lake-
197 abundant Nordic region and complements a recent review on chytrids (Frenken et al., 2017) by

198 summarizing the current status and knowledge gaps on their diversity, richness, and ecological
199 roles in the northern lakes.

200

201 **Materials and Methods**

202 To assess the current diversity status of Chytridiomycota within the Nordic countries, we
203 downloaded all records of chytrid fungi from the GBIF, including environmental samples
204 within the countries Denmark, Finland, Sweden, Norway and Iceland (Abarenkov, 2015,
205 Botanic Garden Meise, 2020, CABI (Centre for Agriculture and Biosciences International),
206 2018, Calabuig, 2014, Dueñas, 2018, Frøslev and Ejrnæs, 2018, Frøslev et al., 2020, Grant and
207 von Konrat, 2019, MGnify, 2019, Ramirez et al., 2020, Telenius, 2016a, Telenius, 2016b,
208 Telenius and Shah, 2018, University of Michigan Herbarium, 2020, Wittzell and Shah, 2020).
209 Due to the differences between the accepted groups within the phylum Chytridiomycota, we
210 classified the records according to both Naranjo-Ortiz and Gabaldón (2019) and Tedersoo et
211 al. (2018) (Table 1). Records belonging to Blastocladiomycetes T. James, Olpidiales Caval.-
212 Sm. and Neocallimastigomycetes M. J. Powell, were removed on the basis that they are not
213 recognized as members of the phylum Chytridiomycota and have all been assigned to separate
214 phyla. As none of the records made by Johnson Jr (1969b) and Johnson Jr and Howard (1968)
215 were included in the GBIF database, Iceland was effectively excluded, due to the five records
216 in GBIF all belonged to Blastocladiomycetes, which is now accepted as Blastocladiomycota
217 T. James (James et al., 2006b).

218

219 **Table 1.** Overview of total observation records of Chytridiomycota across the Nordic countries
220 based on different taxonomic classifications.

221

Country	Records Tedersoo et al. (2018)	Records Naranjo-Ortiz and Gabaldón (2019)	Raw records GBIF
Denmark	569	584	665
Sweden	330	330	398
Finland	186	186	232
Norway	131	134	146
Total	1216	1234	1446

222

223 The GBIF data included environmental samples, human observations, and preserved specimens
224 (Fig 2A). This revealed some systematic differences between the countries (Fig 2B) that can

225 be ascribed to whether large metabarcoding projects have been conducted (e.g [Biowide](#) -
226 Biodiversity in Width and Depth, Denmark) or not. The taxonomic rank was clearly dependent
227 on the sample type (Fig 2).

228

229 **Results**

230 When comparing the two different taxonomic classification systems, some differences were
231 unfolded. At the class level within the Naranjo-Ortiz and Gabaldón (2019) classification
232 system, chytridiomycetes was by far the dominating class across all countries (Fig 3A). The
233 system proposed by Tedersoo et al. (2018) revealed a higher heterogeneity at the class level
234 (Fig 3B). Due to the elevation of Synchytriomycetes, this is the most frequent recorded class
235 in Sweden and Finland sensu Tederso et al. (2018). Rhizophydiomycetes is the dominating
236 class amongst Danish records and is also abundant in Norway and Finland sensu Tederso *et al.*
237 (2018). This class is clearly more associated with environmental samples and is therefore
238 virtually absent in Sweden. However, Denmark had a high number of unclassified records.
239 Notably, Denmark had the overall highest number of records across both classification systems.
240 Big studies such as the abovementioned Danish project Biowide have clearly contributed to the
241 overall increase in chytrid records in terrestrial systems, although many of these cannot be
242 classified below the phylum level. Sweden had the lowest diversity at the class level, and this
243 corresponded well to the low records of environmental samples. Nearly all samples from
244 Sweden are preserved specimens or human observations.

245 The taxonomic classification systems proposed by Naranjo-Ortiz and Gabaldón (2019) and
246 Tedersoo et al. (2018) also differed at the order level. Many records with affinity to the
247 Chytridiales sensu Naranjo-Ortiz and Gabaldón (2019) are affiliated to the Synchytriales sensu
248 Tedersoo et al. (2018). The variation between the diversity observed at the class (Fig 3B) and
249 the order levels within the Tedersoo et al. (2018) classification system is nearly identical. This
250 may indicate very fine-tuned taxonomic resolution at the class level and tentatively to a
251 multitude of undescribed orders within the Chytridiomycota. As new orders are being described
252 in recent years (Karpov et al., 2014), it is not unlikely to assume discovery of new taxonomic
253 entities at lower taxonomic levels. Monotypic microbial taxa are enigmas, as they represent
254 either (1) true phylogenetically isolated entities or (2) indicate lack of species discovery. By
255 using the past fossil records to reconstruct the present taxonomic distribution, monotypic taxa
256 should be expected to be relatively common (Sepkoski Jr, 1978). However, in case of scenario
257 (2), it would be tempting to use higher taxonomic ranks to estimate lower taxonomic (e.g.

258 species) diversity. This is known as “taxonomic surrogacy”, and it implies a predictable
259 relationship between taxonomic ranks, however, subjective rank allocation highly affects
260 diversity measures (Bertrand et al., 2006), and should thus be used with great caution. Using
261 taxonomic surrogacy on the “lumping” (Naranjo-Ortiz and Gabaldón, 2019) and “splitting”
262 (Tedersoo et al., 2018) classification systems will create large systematic differences in the
263 diversity estimates of chytrids, especially because they differ at a very high taxonomic level
264 (class).

265 Approximately 30% of all records could not be assigned at the genus level, and this number
266 increased to over 50% at the species level across the Nordic country records. A total of 29
267 genera comprising 37 species was found (Fig 3C), and *Synchytrium* constituted 30% of all
268 genus records, in which the species *S. anemones* was the most abundant. Notably, the host-
269 specific plant parasite *S. anemones* is visible by the naked eye, making observation of this
270 particular species easy and thus common. Variation of diversity was still observed between the
271 Nordic countries, and genus-level records from Denmark were still more diverse at the lower
272 taxonomic level compared to the three other countries (Table S1), however, at the species level
273 nearly 75% of all Danish and Finnish records could not be assigned. *Synchytrium* was by far
274 the most dominating genus amongst Norwegian and Swedish records amounting to between
275 50-80% of all records in comparison to 30% when combining all four countries, indicating
276 higher abundance of other genera within Danish and Finnish records.

277 Three species were shared amongst the four Nordic countries (Fig 4), and most of the Nordic records
278 were from terrestrial systems. Although there were differences in regard to nature types, land use
279 histories and traditions, many similarities related to geological events, species richness and diversity,
280 life histories, and ecosystem types could be found. For three of the five Nordic countries (i.e. Norway,
281 Sweden and Finland), forests, alpine and arctic soils are common, and these countries should thus be
282 expected to share chytrid diversity.

283

284 **Metabarcoding as a tool for detecting hidden chytrid diversity**

285 *Water systems*

286 Very limited sequence information on zoosporic fungi globally poses challenges to obtaining
287 a robust chytrid tree of life (Naranjo-Ortiz and Gabaldón, 2019). In Northern Europe in
288 particular, the low diversity of records makes a chytrid species estimate very difficult.
289 Moreover, aquatic fungal community data from the Nordic countries using metabarcoding
290 remain relatively scarce (Khomich et al., 2017, Wurzbacher et al., 2020). Notably,

291 Chytridiomycota were shown to be quantitatively the most abundant group (63% of the total
292 reads) in a large survey spanning 77 oligotrophic lakes along a longitudinal gradient in southern
293 Scandinavia targeting the internal transcribed spacer (ITS2) region of the rRNA gene
294 (Khomich et al., 2017). Wurzbacher et al. (2020) have reported that members of the phyla
295 Chytridiomycota and Cryptomycota/Rozellomycota were highly abundant in the surface
296 waters of the groundwater springs in Iceland using ITS metabarcoding. These findings confirm
297 the importance of chytrid fungi in aquatic food webs (Kagami et al., 2014, Sime-Ngando,
298 2012). Most freshwater diversity surveys focusing on cyanobacteria and/or diatoms report the
299 importance of parasitism by chytrids, however, such studies do not include diversity and
300 taxonomy related to these algal parasites (Sime-Ngando, 2012). Khomich et al. (2017) reported
301 that one of the recovered operational taxonomic units (OTUs) had close affinity to the chytrid
302 strain *Rhizophydiales* sp. Chy-Lys2009 (Sønstebø and Rohrlack, 2011), ascribed to the species
303 *Rhizophidium megarrhizum*. Due to the coarse level of resolution, Khomich et al. (2017)
304 identified 47 OTUs within the orders *Rhizophydiales*, *Chytridiales* and *Spizellomycetales* in a
305 small proportion of their initial dataset. This gives an indication of the expected chytrid
306 diversity across lakes in Northern Europe. In comparison, Davis et al. (2018) revealed a total
307 of 57 species within the two lakes in the USA, advocating higher chytrid diversity. Studies
308 within marine systems also report on high species diversity amongst chytrids, especially in
309 coastal and sediment samples (Comeau et al., 2016, Picard, 2017, Richards et al., 2015).
310 Interestingly, chytrids have been reported to even dominate the fungal community in several
311 sites (Hassett and Gradinger, 2016, Richards et al., 2015). Although chytrid parasitism on
312 diatoms and other algae are known in marine systems, a few studies have been conducted
313 highlighting a knowledge gap in the diversity and functional roles of chytrids from marine
314 habitats (Amend et al., 2019, Gutiérrez et al., 2016, Picard, 2017, Richards et al., 2015). Our
315 systematic review of chytrid records in Scandinavia demonstrates how influential
316 metabarcoding is for detecting hidden diversity and that the use of such methods affects the
317 taxonomic rank identified within the habitats.

318

319 *Soil systems*

320 Although many of the chytrids have been described from aquatic systems, a number of chytrid
321 species have also been recorded in soil numerous times across a variety of terrestrial systems,
322 usually in minor abundancies and seemingly more dominant in high-elevated soils (Blaalid et
323 al., 2012, Freeman et al., 2009, Jimu et al., 2018, Schmidt et al., 2013, Tedersoo et al., 2014).

324 Soil within such areas may be perceived as extreme conditions as it can be saturated with water
325 for longer periods such as during winter (Freeman et al., 2009). In such cases chytrid
326 dominance could be explained through these organisms' way of life. Due to the low chytrid
327 records, and often low taxonomic resolution of such records, these fungi are not regarded as a
328 highly important ecological group compared to Asco- and Basidiomycota. However, chytrids
329 are known to be one of the primary decomposers of organic matter within such habitats, and
330 their adaptation to this complex niche makes them important players within soils (Gleason et
331 al., 2012b).

332

333 **Chytrid diversity – future perspectives**

334 All data related to Chytridiomycota in Barcode of Life Data system (BOLD) were mined from
335 the non-curated database GenBank (<http://www.boldsystems.org>). In total, BOLD includes 276
336 sequences comprising 76 chytrid species worldwide. The great majority of Chytridiomycota
337 has not been cultured and studied, and many assigned clades are classified as “uncultured” in
338 sequence databases (Grossart et al., 2016). Khomich et al. (2017) states that the lack of ITS
339 information within databases explains why a high proportion of unidentified sequences were
340 obtained within their study. Another study has reported the poor database (ITS marker)
341 representation for the fungal communities in aquatic (freshwater and marine) and soil
342 ecosystems (Khomich et al., 2018). The choice of marker is highly important, and it might
343 explain the described diversity of chytrids across studies (Khomich et al., 2018, Khomich et
344 al., 2017, Lepère et al., 2019, Wurzbacher et al., 2019). The most commonly used marker
345 within soil systems is the ITS since the focus of many studies is general diversity and richness
346 in fungal communities (Blaalid et al., 2013, Buee et al., 2009, Li et al., 2020, Lindahl et al.,
347 2013). Aquatic and marine systems surveys are less monogamous to the ITS marker, and here
348 both the small ribosomal subunit (SSU) and the large ribosomal subunit (LSU) have been
349 applied together with the ITS (Edgcomb et al., 2011, Heeger et al., 2018, Picard, 2017,
350 Wurzbacher et al., 2016). Although the ITS is the chosen barcode marker for fungi, the high
351 proportion of unidentified sequences and therefore inability to recover taxa from a mock fungal
352 community may reflect poor ITS database coverage (Heeger et al., 2018, Khomich et al., 2017).
353 Biases in regard to primer and database choice are known to affect functional group richness
354 for some classes of fungi thus potentially distorting ecological patterns (George et al., 2019).
355 The full length ITS marker is not known to generate bias against Chytridiomycota (Anderson
356 et al., 2003). Still, most metabarcoding studies choose between the ITS1 and ITS2. Combining

357 the 5.8S with the ITS2 demonstrates superior classification of species with a cryptic taxonomy
358 at higher level classifications (Heeger et al., 2018). The continuation to use metabarcoding in
359 research is to be expected, however, the lack of a good-resolution taxonomic marker encounters
360 a challenge within the chytrid group assessment. The high number of “dark matter fungi”
361 reported from such studies serves as an indication of high diversity across habitats. Chytrid
362 distribution across the Nordic countries illustrates the need for a good and generally accepted
363 chytrid backbone. In addition, within the early diverging fungal lineages new phyla are still
364 being proposed, and as more sequence data are being generated the UNITE approach in
365 creating species hypotheses may contribute to the overall chytrid backbone (Nilsson et al.,
366 2019).

367

368 **Acknowledgements** We acknowledge the Norwegian Biodiversity Information Centre for
369 financial support through the grant 25/19 “AquaFun”. We also thank two anonymous reviewers
370 for their valuable suggestions on the improvement of the manuscript.

371 **Author contributions** R.B directed the project and performed the analyses. R.B and M.K
372 wrote the manuscript.

373 **Conflicts of interests** The authors declare no conflict of interests and confirm full compliance
374 to research ethics.

375

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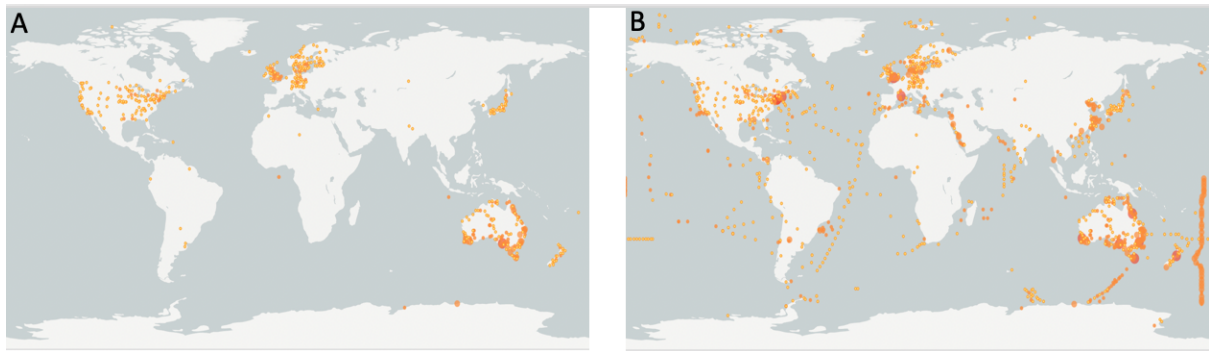
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648 **Figure legend**

649 **Fig. 1** Occurrence map of Chytridiomycota (sensu James et al 2006) depicting (A) only
650 preserved specimens and (B) preserved specimens, environmental samples and human
651 observations. Maps are downloaded directly from the Global Biodiversity Information Facility
652 (GBIF; <https://www.gbif.org>), February 2020.

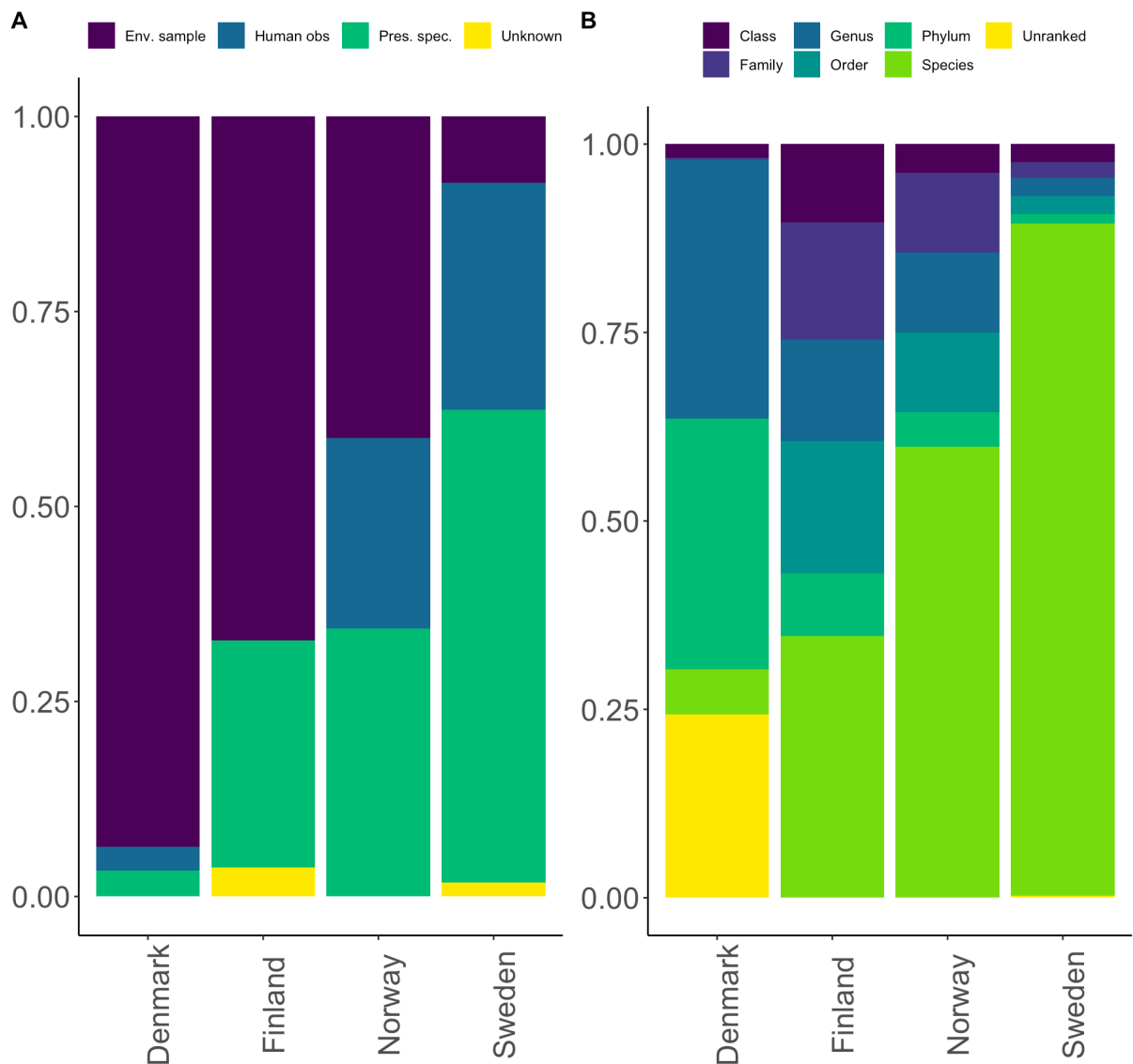


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Fig. 2 Overview (in %) of (A) which sample type is most abundantly found across the four Nordic countries and (B) at what taxonomic rank affiliated with different sample types.



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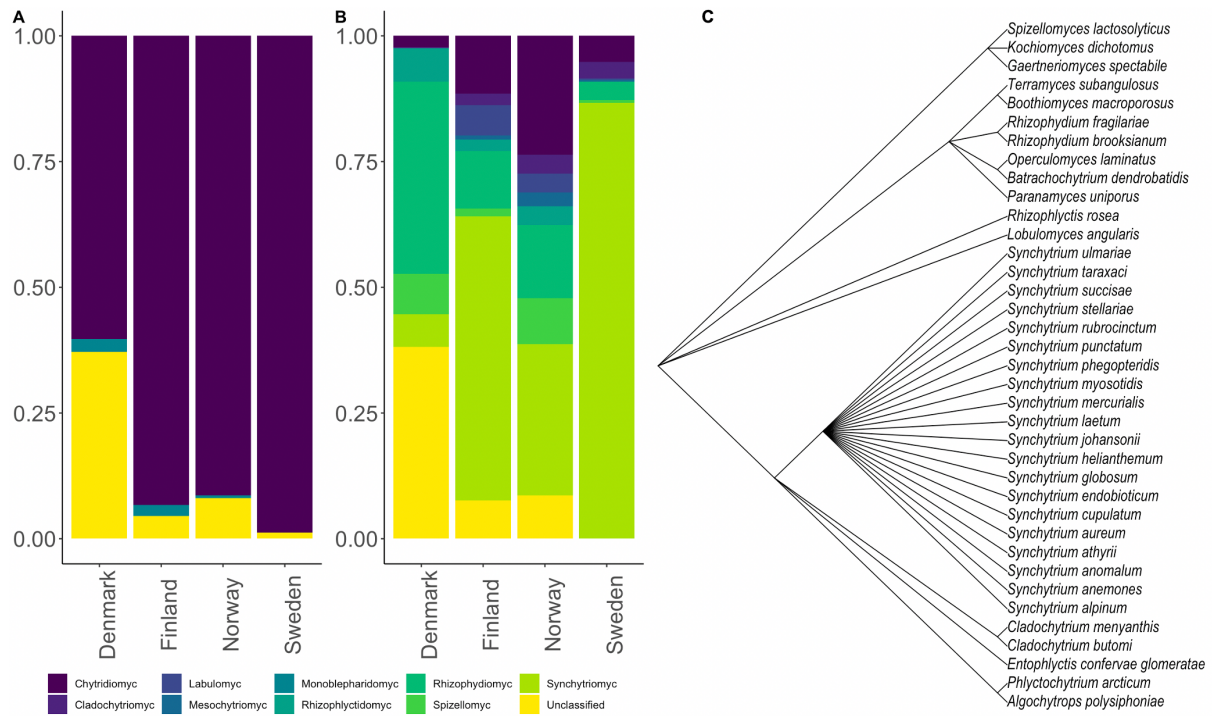
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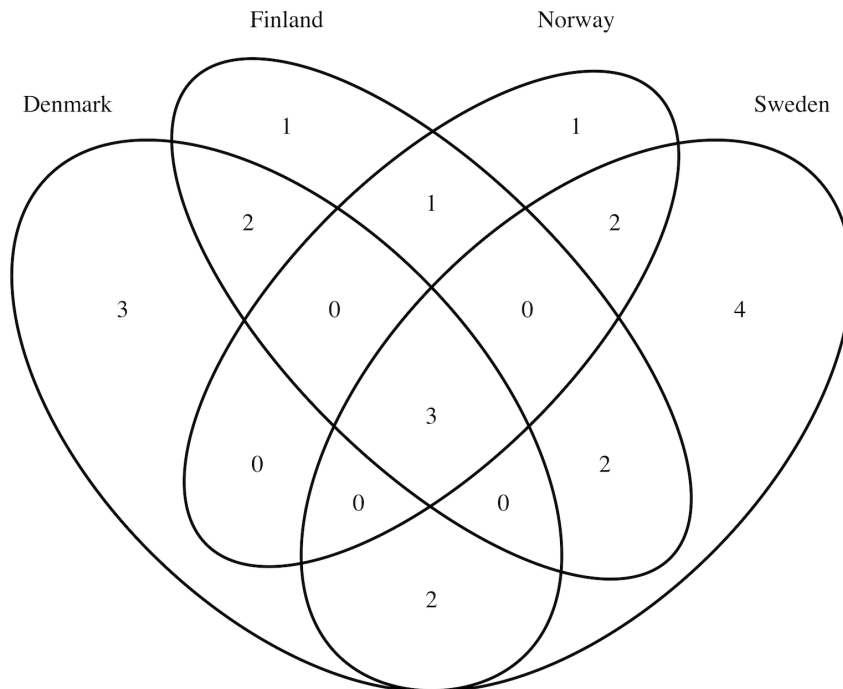
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Fig. 3 Overview of the class-level records between the Nordic countries according to the classification systems of (A) Naranjo-Ortiz and Gabaldón (2019) and (B) Tedersoo et al. (2018). (C) Cladogram of the species belonging to Chytridiomycota records across the Nordic countries according to the classification systems of Naranjo-Ortiz and Gabaldón (2019).



661

662 **Fig. 4** Venn diagram depicting shared chytrid species across the four Nordic countries
 663 Denmark, Sweden, Norway and Finland.



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665 **Table S1** Complete data records of Chytridiomycota downloaded from the Global Biodiversity
 666 Information Facility (GBIF).

gbifID	class	order	family	genus	species	taxonRank	countryID	Year	basisOfRecord
2442363747	Chytridiomycetes	Chytridiales	Chytriomycetaceae	Rhizoclostridium		GENUS	DK	2009	MATERIAL_SAMPLE
2244194347	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2019	HUMAN_OBSERVATION
2242671626	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2019	HUMAN_OBSERVATION
2238547756	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2018	HUMAN_OBSERVATION
2238466973	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium taraxaci	SPECIES	DK	2016	HUMAN_OBSERVATION
2238446300	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2016	HUMAN_OBSERVATION
2238410914	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2015	HUMAN_OBSERVATION
2238324265	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	2009	HUMAN_OBSERVATION
2238264527	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	1987	PRESERVED_SPECIMEN
2238263247	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	1987	PRESERVED_SPECIMEN
2238209014	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2013	HUMAN_OBSERVATION
2238144021	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	2012	HUMAN_OBSERVATION
2238143844	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	2012	HUMAN_OBSERVATION
2238143723	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	2012	HUMAN_OBSERVATION
2238006987	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2006	HUMAN_OBSERVATION
2237981118	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	2005	HUMAN_OBSERVATION
2237955935	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2011	HUMAN_OBSERVATION
2237862063	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2019	HUMAN_OBSERVATION
2237860626	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2019	HUMAN_OBSERVATION
2237859900	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	2019	HUMAN_OBSERVATION
1988708677	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium globosum	SPECIES	DK	1906	PRESERVED_SPECIMEN
1949671888	Chytridiomycetes	Chytridiales	Chytridiaceae	Phlyctochytrium		GENUS	DK	2014	MATERIAL_SAMPLE
1930009436	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium globosum	SPECIES	DK	1906	PRESERVED_SPECIMEN
1929820284	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium stellariae	SPECIES	DK	1878	PRESERVED_SPECIMEN
1840640677	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	1882	PRESERVED_SPECIMEN
1840640664	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	NA	PRESERVED_SPECIMEN
1840640630	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium stellariae	SPECIES	DK	1878	PRESERVED_SPECIMEN
1840640617	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium stellariae	SPECIES	DK	NA	PRESERVED_SPECIMEN
1585885550	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	1903	PRESERVED_SPECIMEN
1585884386	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium globosum	SPECIES	DK	1904	PRESERVED_SPECIMEN
1585884030	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	1892	PRESERVED_SPECIMEN
1585884015	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	1892	PRESERVED_SPECIMEN
1585883497	Chytridiomycetes	Chytridiales	Cladochytriaceae	Cladochytrium	Cladochytrium menyanthis	SPECIES	DK	1991	PRESERVED_SPECIMEN
1148296071	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium aureum	SPECIES	DK	1912	PRESERVED_SPECIMEN
1135258668	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium globosum	SPECIES	DK	1904	PRESERVED_SPECIMEN
1052171113	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	1882	PRESERVED_SPECIMEN
1042891635	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium mercurialis	SPECIES	DK	NA	PRESERVED_SPECIMEN
1042891634	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium myosotidis	SPECIES	DK	1882	PRESERVED_SPECIMEN
126942647	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium globosum	SPECIES	DK	NA	UNKNOWN
125757378	Chytridiomycetes	Chytridiales	Synchytriaceae	Synchytrium	Synchytrium anemones	SPECIES	DK	1987	PRESERVED_SPECIMEN
1949696641	Monoblepharidomycetes	Monoblepharidales	Monoblepharidaceae	Monoblepharis		GENUS	DK	2014	MATERIAL_SAMPLE
1949693138	Monoblepharidomycetes	Monoblepharidales	Monoblepharidaceae	Monoblepharis		GENUS	DK	2014	MATERIAL_SAMPLE
1949693105	Monoblepharidomycetes	Monoblepharidales	Monoblepharidaceae	Monoblepharis		GENUS	DK	2014	MATERIAL_SAMPLE