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How citizen science boosted primary knowledge on fungal biodiversity in Denmark



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ABSTRACT

The Danish Fungal Atlas was a citizen science project aiming to map Danish macrofungi over five years (2009–13). The atlas contributed > 235,000 records of fruit-body forming Basidiomycota, adding to about 195,000 fungal records from earlier periods. The new records increased the average number of species known per 10 km \times 10 km grid cell by 75% from 125 to 218 species. We recorded 197 species as new to Denmark, extending the number of known basidiomycote species by 7%. At least 15 species appeared to be new to science. Among the new Danish records, species with northern distribution ranges were significantly overrepresented, in marked contrast to climate change predictions. Species with inconspicuous or subterranean fruit bodies were overrepresented among both the new Danish species and those only recorded before the project period, indicating low recording probability to be an important driver for the turnover in species scientists guided by professional mycologists and 2) improved taxonomic knowledge. Summarizing over the last 100 years, an exponential increase in known macrofungal diversity in Denmark is evident, suggesting that we are still far from having a complete overview. This is striking, considering that Denmark is among the best-studied land areas on the globe. We conclude that citizen science projects, if appropriately designed, have a huge potential to boost primary knowledge on fungal biodiversity.

1. Introduction

While life on Earth faces a sixth mass extinction, millions of species still await description and cataloguing by science, and may be lost before we even learn about their existence (Mora et al., 2011; Lees and Pimm, 2015). This is especially true for hyperdiverse taxa, such as fungi and arthropods (Scheffers et al., 2012). The fungal kingdom is probably the major branch on the tree of life with the biggest taxonomic deficit, i.e. lowest proportion of total species number known and catalogued. Current global estimates of fungal species numbers vary in the range of 2.2 to 166 million species, of which only around 120,000 are formally described (Hawksworth and Lücking, 2017; Larsen et al., 2017). The variation in estimates is partly due to difficulties in defining what "a fungus" is, as some basal groups still have a disputed kingdom affiliation. However, it is important to recognize that the fungal kingdom

encompass everything from unicellular microorganisms to some of the largest organisms on the globe (Petersen, 2013), with huge variation in knowledge levels. Most unknown diversity is expected among microfungi in poorly explored habitats, including living animal and plant tissues. At the other extreme, fruit-body forming Basidiomycota are markedly better known than other fungal groups, with Europe being particularly well investigated (Schmit and Mueller, 2007).

Apart from progress resulting from traditional taxonomic studies, new fungi are mainly discovered using traditional inventory methods in poorly studied areas and habitats, or by massive sequencing of environmental samples (Hawksworth and Lücking, 2017; Truong et al., 2017). In addition, many unrecognized novel species have already been collected and preserved in fungaria, awaiting discovery or formal description (Yahr et al., 2016). These approaches to increasing knowledge are all expert driven, and new taxonomic discoveries rarely involve the

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Received 27 February 2019; Received in revised form 27 June 2019; Accepted 5 July 2019 Available online 22 July 2019 0006-3207/ © 2019 Elsevier Ltd. All rights reserved. broader public, even if inclusion of amateurs could increase the relevance and impact of new discoveries considerably (Barron et al., 2015). Traditionally, fungi have been considered more difficult to study for amateurs than for example plants, birds, butterflies and mammals, because of identification difficulty, limited knowledge and high species diversity. Further, the common, but flawed, cultural perspective that fungi lack charisma and mainly cause harm to other organisms has limited their appreciation as relevant, positive targets for biodiversity conservation (Griffith, 2012; Heilmann-Clausen et al., 2015). Fungi are underrepresented in both citizen science and mainstream biodiversity science (Theobald et al., 2015), despite their overarching importance in ecosystem processes and also for the livelihood of people in many rural regions (Heilmann-Clausen et al., 2015). However, perspectives are changing, and the appreciation of fungal diversity as a relevant and feasible topic for citizen science is growing (Halme et al., 2012; Andrew et al., 2017). So far, fungal citizen science data has mainly been explored scientifically to investigate phenological and distributional changes of macrofungi as a response to global change (e.g. Gange et al., 2007; van Strien et al., 2017). More recently, it has been used to disentangle large-scale biodiversity patterns (Andrew et al., 2018; Ordynets et al., 2018), species interactions (Heilmann-Clausen et al., 2016) and trait evolution (Kauserud et al., 2011), highlighting a potential of fungal citizen science data in basic research. While the above research is based on data collected using a simple, mass-participation approach as defined by Pocock et al. (2017), a few recent fungal citizen science projects have been developed using a more elaborate and targeted approach. For instance, mycologists at Kew Gardens recently launched their Lost and Found Fungi project, aiming to engage the public in (re-)discovering 100 little known, but potentially threatened species in the UK (Douglas, 2016).

Denmark has a long tradition of both professional and amateur mycology. The Danish Mycological Society was founded in 1905 with a focus on the amateur community of field mycologists. It currently has around 2000 members out of a 5.5 million population, which is a relatively high proportion compared to many other European countries (Dahlberg et al., 2010). Historically, the works of Emil Rostrup (collated by Lind, 1913), Jakob E. Lange (1935-40) and Mads Peter Christiansen (1959-60) were pioneering contributions to research on European plant pathogens, agarics and corticioid fungi, respectively, and more recently the works edited by Hansen and Knudsen (1992-2000) and Knudsen and Vesterholt (2008) have provided stateof-the-art identification keys and standardized species descriptions for the basidiomycotes of northern Europe. The first Danish web-based recording scheme for fungi was launched in 2005 (Lange, 2006), but already from the early 20th century, coordinated efforts were made to collect fungal records from forays and field trips under the auspices of the Danish Mycological Society (Lange, 1974). Despite these efforts, it was well known, prior to the Danish Fungal Atlas project here reported, that the knowledge of the present Danish funga was incomplete. A press release before the project launched in 2009, estimated the Danish funga to include about 2700 species within the macrofungal target groups. Although the project was expected to enhance knowledge on Danish macrofungi considerably, it soon became clear that the potential for novel biodiversity discoveries was much larger than expected, when > 50 records of species new to the Danish funga were recorded in the first year alone (Vesterholt et al., 2010).

There is overarching consensus that global warming will affect species distribution patterns (Bellard et al., 2012; Garcia et al., 2014), and even though evidence of climate driven range shifts in macrofungi is still limited (Gange et al., 2018), we hypothesized climate change to be an important driver for the many species recorded as new to Denmark. To test this, we explored to what degree species recorded as new to Denmark during the Fungal Atlas project, emerged as a result of northward range expansion, potentially caused by climate change, or simply reflected increased effort and taxonomic knowledge. Similarly, we explored if species only recorded before the atlas period were

disappearing, again with climate warming or other habitat changes as possible causes. More exactly, we tested the importance of distribution range patterns, fruit-body type and year of scientific description as explanations for novel species discoveries and non-recovery. In addition, we investigated spatial patterns of novel species discoveries and related these to changes in recording activity from before the atlas period. We expected southern species to be overrepresented among the new Danish species. In addition, we expected positive effects of the intensive sampling and identification effort during the Atlas period.

2. Material and methods

The Danish Fungal Atlas was a 5-year citizen science project running from 2009 to 2013 aiming to collect data on the distribution and ecology of all fruit-body forming Basidiomycota in Denmark, but open also to records of Ascomycota and other fungal groups. The project was a collaboration between the Natural History Museum of Denmark, the Department of Biology at the University of Copenhagen, the Danish Mycological Society and MycoKey (http://www.mycokey.com). The project was open to anyone willing to report their fungal recordings, with no detailed guidelines on reporting and no geographical constraints. However, competitions were designed to encourage participants to report from understudied regions. Also, nine week-long recording camps were organized in poorly sampled parts of the country. At these camps, professional mycologists and amateurs worked together, with a common goal to improve geographical coverage, and to train amateurs in fungal identification. Similarly, the web-recording platform involved interactive record-specific forum functions, allowing professionals and amateurs to interact in the identification process. The Fungal Atlas project involved a rigorous validation procedure for fungal species identification. At the beginning of the project, 2490 species (approximately 84% of known Danish species in the target groups) were coded with requirements for validation (e.g. description of smell or taste, photograph or dried voucher specimen, depending on the difficulty of obtaining a correct identification). As a result, volunteers sent several thousand dried specimens to professional experts for verification. In total, >400 people contributed to the project, of which c. 100 can be described as core contributors, each supplying at least 100 records.

The Fungal Atlas platform represents an extension of an already existing internet platform for recording fungi in Denmark established in 2005, and is still available in an updated version at https://svampe. databasen.org/. In addition to enabling reporting of new fungal records, older data were imported from private databases, published and unpublished foray lists, preceding web-fora and news groups. Data for the current analyses were extracted on December 20, 2016, including all approved records of fruit-body forming basidiomycotes from Denmark, recorded in the official Fungal Atlas period or before. The older data were subject to the same validation procedures as data recorded during the official Fungal Atlas period. Records annotated to names with doubtful taxonomic status were omitted from the dataset. The historical and new data are therefore equally reliable.

2.1. Species attributes

Firstly, we categorized all species in the dataset into morphological groups according to 12 fruit-body types (see Appendix S1). Secondly, we extracted known species-specific distribution patterns in Europe from the literature. For this, most species were scored based on their frequency across climatic zones (arctic/alpine, subarctic, boreal, hemiboreal, nemoral) according to Hansen and Knudsen (1992–2000) and Knudsen and Vesterholt (2008). However, for many corticioid fungi, Bernicchia and Gorjon (2010) was the main source, while special literature was consulted for rare species across all species groups. A total of 433 species were classified as *northern* because they were more common in climate zones north of Denmark (hemiboreal to arctic) or

because they were only recorded north and/or east of Denmark. Similarly, 693 species were classified as *southern* because they were assessed as more common in the nemoral zone than in more northern zones, or only recorded south and/or west of Denmark. The remaining 1886 species with no distinct gradient in frequency across climate zones or in geographical space were classified as *ubiquitous*. The inclusion of eastern and western distributions in the *northern* and *southern* distribution zones, respectively, was based on the prediction that climate and vegetation zones are mainly shifting from SW to NE in Europe (e.g. Hickler et al., 2012). Finally, the year of scientific description was extracted from www.indexfungorum.org for all species based on their basionym. The full dataset is provided as Appendix S2.

2.2. Data analysis

All statistical analyses were conducted in R version 3.4.2. (R Core Team, 2017). Species were divided into three categories based on their recording period: New, if recorded for the first time in Denmark during the Fungal Atlas period (2009-2013), old, if only recorded before the Atlas period, and both, if recorded in both periods. To test for geographical patterns in the recording of *new* and *old* species, a negative binomial model was fitted using the MASS package (Venables and Ripley, 2002), based on data geographically aggregated to a $10 \text{ km} \times 10 \text{ km}$ grid (n = 642). This grid is the same as that used in several other Danish atlas projects (e.g. bird atlas, mammal atlas). The number of records of new and old species per grid cell was used as dependent variables. The total number of records per grid cell in the new and old period, respectively, was used, as a measure of recording activity, together with the north-east coordinate of the grid cell midpoint (in kilometers counting from an origin point in the extreme southwest of Denmark, based on the UTM grid) as predictor variables. The model was fitted using the "glm.nb" call, increasing the maximum number of allowed iterations to 100 using the specification "control = glm.control(maxit = 100)". Subsequently, a multinomial logit regression model was fitted to test for the influence of fruit-body type, distribution and year of description on recording periods using the mlogit package (Croissant, 2012). Odds ratios were calculated using species found in both recording periods as reference in the response variable, and ubiquitous and agarics as reference stages for the two independent categorical variables (distribution and fruit-body type).

As a supplement to statistical analyses, the number of target species known in Denmark over time was summarized based on the most important checklists, monographs and identification books for basidiomycotes in Denmark. For several period and species group combinations, species numbers were extrapolated to give a more realistic, yet approximate, representation of the growth in the total number of species accepted as Danish over time (see Appendix S3). An exponential trend line was fitted to the data using default settings in MS-Excel.

3. Results

During the atlas period (2009–2013) 244,772 records of Basidiomycota were accepted in the database, of which 236,204 (96%) were validated at the species level. Almost 80% of these records

represented 438 widespread, characteristic and common species, for which no validation requirements were defined. 13,108 records (6%) were re-determined by the appointed expert validators, of which almost 8500 represented species requiring validation, while 4600 records represented species without validation requirements. This corresponded to 18% and 2% of all validated records in each category respectively. Besides the new data, 195,080 records were imported from older sources, yielding a grand total of 431,284 validated records for 3012 species of fruit-body forming basidiomycotes. Hence, roughly 45% of the records in the full dataset were from before the atlas period, while 55% were produced during the atlas period. Across all 10 km \times 10 km grid cells, 59,932 records from the atlas period represented species not previously known from particular grid cells, corresponding to 25% of all new validated records. These records increased the average number of species recorded per grid cell by 74%, from 125 to 218 species.

A total of 197 species were recorded as *new* to Denmark during the atlas period, increasing the number of known species in Denmark from the target group by 7% from 2815 to 3012 species. More than 40 atlas volunteers contributed with records of *new* species to Denmark. A total of 510 species, which had records from before the atlas period, were not rediscovered and reported in the Atlas, and are hence denoted *old* species.

Of all recorded species, 28 were formally described as new to science during the atlas period. However, some of these had actually been recorded before the atlas period under other or temporary names, and were hence not counted as new to Denmark in the present study. Two species, *Hebeloma griseopruinatum* and *Cortinarius koldingensis*, were formally described based on type material collected during the atlas period (Eberhardt et al., 2013; Frøslev et al., 2015). In addition, fifteen morphologically well-differentiated species recorded in the atlas period could not be assigned to known species and are counted as *new* Danish species in this paper, even though they still await formal scientific description.

3.1. Effects of activity and geography

The model testing for signals of geography and activity on the presence of species unique to each recording period, showed a highly significant effect of recording activity per grid cell in each time-period. *Old* species were strongly overrepresented in grid cells with high recording activity in the period before the Fungal Atlas, while *new* species were overrepresented in grid cells with many records during the atlas period. A signal of geographical location was only evident for *old* species, which were slightly but significantly overrepresented towards the northeast (Table 1).

3.2. Species specific attributes

The model testing for species-specific attributes associated with recording periods was highly significant (Likelihood ratio test: chisq = 605.71, *p*-value < 2.22e-16) and showed significant effects of all predictor variables, explaining about 15% of the variation in the response variable (McFadden's $R^2 = 0.15$). Species with a *northern* distribution were significantly overrepresented among both *old* and *new*

Table 1

Summary of negative binomial models predicting the number of macrofungal species recorded per 10×10 km grid cell in each of the two recording periods, in relation to the geographical location and number of records per grid cell per period.

Variable ^a	Old species			New species		
	Sign	Z-value	р	Sign	Z-value	р
No. of records (before Atlas period, <2009)	+	15.234	< 0.0001	+	2.204	0.0275
No. of records (in Atlas period, 2009–13)	-	1.205	0.2281	+	6.771	< 0.0001
Northeasting	+	2.466	0.0137	+	0.234	0.8151

^a The intersect was negative and highly significant in both models, which each had 632 degrees of freedom.

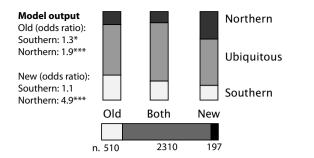


Fig. 1. Relative proportions of *southern*, *northern* and *ubiquitous* distribution patterns for macrofungal species recorded only in the *old*, *new* or in *both* recording periods (indicated as proportions of the total species pool in the horizontal bar; *old*: white, *both*: pale grey; *new*: black). Odds ratios were calculated based on the Mlogit model parameter estimates keeping *ubiquitous* distribution and *both* periods as reference levels. Significance levels: *p = 0.05-0.01, **p = 0.01-0.001, *** < 0.001. Note that the bars show raw proportions, and hence the somewhat lower proportion of *southern* species among the *new* species, compared to the control (*both*), corresponds to a slightly higher odds ratio in the full model accounting for the additional model terms.

species, being 1.9 and 4.9 times more numerous, respectively, than in the reference group. Species with a southern distribution were slightly overrepresented in the same groups, but only significantly so for species found only in the *old* period (Fig. 1).

Several fruit-body types were significantly overrepresented among the *old*, and to a lesser extent among the *new* species (Fig. 2). Overrepresentation among *old* and *new* species was particularly pronounced for species groups with inconspicuous fruit-body types, e.g. mycoparasitic gall formers, false truffles and corticioid fungi, while boletes were found more often in *both* periods than agarics, forming the reference group (Fig. 2).

Finally, the effect of description year in the model was highly significant (p < 0.0001) for both *old* and *new* species, compared to species found in *both* periods. The average description year for species found in *both* periods was 1873, while it was 1920 and 1953 for *old* and *new* species respectively.

The accumulation curve for the number of species of fruit-bodyforming Basidiomycota known in Denmark over the last century, based on published sources and recordings in the current project, showed a continuous increase, with the best fit provided by an exponential

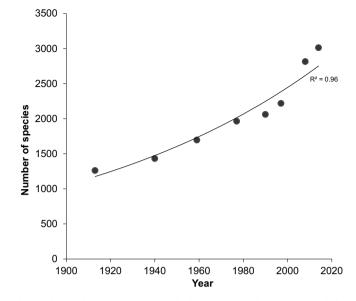


Fig. 3. The number of species of fruit-body forming Basidiomycota recorded in Denmark over time based on published sources and the current study (for details see Appendix S3), with a fitted exponential line.

function (Fig. 3), with no sign of saturation, or even a stagnating rate of increase.

4. Discussion

In this study, we documented a huge increase in the recording activity of fungi in Denmark, a country that was mycologically well-studied already. This remarkable achievement was the direct result of a citizen science project, the Danish Fungal Atlas. The five years of effort to record Danish fungi resulted in almost 60,000 new grid cell $(10 \text{ km} \times 10 \text{ km})$ with species records and 197 species new to the Danish funga. Records of these new Danish species were contributed by 40 different recorders, who all shared the experience of increasing the known species diversity in Denmark. A main aim of the project was to increase the awareness and knowledge of fungi in Danish nature conservation. This was achieved and data have been successfully integrated in national conservation planning, including high nature value maps (Johannsen et al., 2015) and systematic conservation planning for

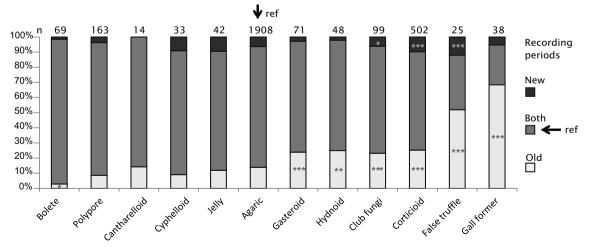


Fig. 2. The relative proportions of species recorded only in the *old*, *new* or in *both* recording periods indicated for each of the twelve macrofungal species group defined based on fruit-body morphology (see Appendix S1). The total number of species per group is indicated above each column. Odds ratios were calculated based on the Mlogit model parameter estimates, keeping the fruit-body type *agarics* and the recording period *both* as reference levels. Significance levels: * = 0.05-0.01, ** 0.01-0.001, ** < 0.001.

forest biodiversity based on complementarity (Petersen et al., 2016, 2017), which are both under partial implementation in current national conservation strategies. Further, the collected data serves as a muchimproved basis for ongoing assessments of red-list status for Danish organisms to be published in 2020. Data has also been used for scientific studies (including Andrew et al., 2017, 2018; Flensted et al., 2016; Geldmann et al., 2016; Heilmann-Clausen et al., 2016) and, recently, a popular science book in Danish has provided a comprehensive overview of the project results with a strong focus on practical conservation of important fungal habitats (Heilmann-Clausen et al., 2019).

4.1. Lost and found fungal species

As climate warming is already affecting Denmark, we expected turnover in the recorded species pool to show a signal of northward range expansions (cf. Bellard et al., 2012; Garcia et al., 2014). However, species recorded as *new* to Denmark showed no tendency to be predominantly *southern*, while unrecorded species previously known from Denmark (i.e. *old* species), were not predominantly *northern*. Therefore, climate warming could not be identified as the main driver of the observed temporal turnover in recorded species.

One obvious pattern in our data was that species with high detection probability, i.e. producing conspicuous fruit-bodies, including agarics, boletes, polypores and cantharelloid fungi, tended to be recorded both prior to the atlas and during the atlas period. In contrast, species with lower detection probability, including corticoids, truffles and club fungi, were significantly overrepresented among both old and new species. Further, new species were predominantly recorded from grid cells with high activity in the atlas period, while unrecorded species were overrepresented in grid cells with high activity before the atlas period, but not during the atlas period. This observation emphasizes the interaction of search effort and detection probability, as also emphasized in other studies (e.g. Lõhmus, 2009; Abrego and Salcedo, 2015). In some fungal groups, the sheer lack of both professional and amateur expertise appears to be a strong limiting factor for keeping track of biodiversity, even in a small and well-explored country like Denmark. Thus, for the often cryptic, intrahymenial gall formers, the overrepresentation among the old species can be ascribed to the lifelong devotion to this group by the amateur mycologist Knud Hauerslev (1905–2000), who described ten species in this group as new to science based on Danish collections. Of these, several have, to our knowledge, not been reported anywhere else on the globe, reflecting that these species are difficult to record and hugely understudied, despite their interesting ecology, partly as intrafungal biotrophs (e.g. Spirin et al., 2016).

For two other groups that were overrepresented among the old species (hydnoids, especially species in the Thelephorales, and gasteroids), we believe the apparent species loss represents real biological changes. Both hydnoids and gasteroids have been shown to be very sensitive to eutrophication and acidification of top soil layers (Arnolds, 1991, 2010; Olsson et al., 2010). Indeed, recent research has shown nitrogen deposition to be a major driver of fungal community composition change among both ectomycorrhizal (Van der Linde et al., 2018) and decomposer fungi (Andrew et al., 2018) at the European scale. With nitrogen loads in most of Denmark being beyond thresholds identified in these studies, distinct changes to the funga are to be expected. Monitoring data have evidenced decreasing soil pH and increasing C/N ratios in some terrestrial habitat types in Denmark (Nygaard et al., 2016), which suggest that the reported decline in hydnoid and gasteroid fungi may indeed be related to changes in soil chemistry.

4.2. Knowledge, habitat maturation and geographical signals in recorded species pool turnover

Even if increasing sampling activity and knowledge appeared to be

the main drivers in novel fungal species discovery in this study, the overrepresentation of species with a *northern* rather than *southern* distribution among the *new* Danish species is surprising and counterintuitive. One contributing factor to the lack of such trends in our dataset could be that proven climate warming in Denmark (Danish Ministry of Climate and Energy, 2016), is counteracted by increased stocking of Danish forests (Nord-Larsen et al., 2016). This evidently has a cooling effect on the microclimate near the ground, which delays biotic changes in the forest floor biota as a response to climate warming (Frenne et al., 2013). This effect is rather limited, and even if it may explain why southern species were not recorded as new to Denmark at the expected level, it does not explain the overrepresentation of northern species among the *new* Danish species records in our study.

Availability of literature is a potential explanation for the overrepresentation of northern species. Just prior to the launch of the Atlas project, Funga Nordica (Knudsen and Vesterholt, 2008) was published, providing updated identification keys for major groups of Nordic Basidiomycota based on recent and ongoing taxonomic research in Scandinavia. The identification keys included many recently described or reinterpreted species mainly known from the Nordic countries, lacking from previously used identification guides, mainly issued in central and western Europe (e.g. Moser, 1983; Bas et al., 1990 (and later volumes); Breitenbach and Kränzlin, 1981-2006). Thus, Funga Nordica not only improved species identifications in several difficult species groups, but also inspired the focusing of fungal recording in boreal habitat types, such as willow scrub and coniferous woodlands. Based on this, we suggest increased knowledge to be a main driver for the counterintuitive geographical signal in the species turnover recorded during the atlas period.

A signal of increased knowledge level is also evident because the more recently described species are strongly overrepresented among both *old* and *new* species, when controlling for fruit-body type. Compared to the "classic" species described by mycologists in the 18th and 19th centuries, recently described species tend to be less wide-spread and characteristic, and hence less likely to be recorded by amateur mycologists. However, a true effect of habitat maturation or delayed establishment from source populations in Fennoscandia cannot be ruled out. Coniferous woodlands in Denmark all result from plantations established during the last 200 years (Flensted et al., 2016), while willow scrub has expanded a lot over the last century due to abandonment of grazing, haymaking and peat extraction in wetlands. Most likely, this has created new niches for macrofungi, which have gradually been colonized by fungi with a mainly boreal distribution.

4.3. National and global estimates of macrofungal biodiversity

It is generally accepted that European basidiomycote macrofungi are far better studied than any other large group of fungi. Schmit and Mueller (2007) rather conservatively estimated the taxonomic deficit for macrofungi in Western Europe to about 50 species (1% of known species diversity at that time). Within Europe, Denmark is arguably among the best-studied countries in mycological terms. It is a small country and less biologically rich than most other countries in Europe, due to intensive land use, very modest elevation gradient and no wilderness (Hallanaro and Pylvänäinen, 2001). In this light, it is intriguing that the Danish Fungal Atlas contributed almost 200 new species to the Danish funga, including several species new to science, and overall contributed to a continued exponential growth in known national macrofungal species richness over the last century. Denmark obviously does not host an infinite number of macrofungal species, and the curve has to level off at some point.

Recent taxonomic studies, utilizing DNA markers as a supplement to ecological and morphological data, have shown that previous estimates for macrofungal diversity in Europe is hugely underestimated, and it is more the norm than an exception that taxonomic treatments and monographs of rather well studied fungal genera increase the known diversity by 30–100% (e.g. Jeppson et al., 2017; Niskanen et al., 2018). Within several less well-studied groups of macrofungi e.g. corticoids, the taxonomic deficit is much larger. For instance, van der Linde et al. (2018) recorded 49 OTUs in the genus *Piloderma* across 103 European forest plots, compared to seven species accepted in the most recent treatment of the genus (Bernicchia and Gorjon, 2010).

With increasing taxonomic effort and the fruitful combination of classic taxonomy and DNA based work, including data from environmental samples, we predict that we may reach a sigmoid levelling off, of the so far exponentially increasing Danish macrofungal species number, especially if a fruitful collaboration between amateur and professional mycologists is secured.

4.4. Future perspectives

Overall, we see a huge potential for citizen science in basal exploration of biodiversity, both as unstructured projects, as in the present case, and in the form of dedicated projects with a more specific scope. This could include DNA barcoding, as already practiced in several amateur mycological clubs in North America, both as a tool to speed up identification of difficult specimens and as a tool to unravel difficult species complexes (Sheehan, 2017). Hereby, citizen science could be developed as citizen taxonomy projects (Jisming-See et al., 2016). If designed appropriately, such projects may not only secure more efficient sampling and better geographical coverage in the often frustratingly short time-windows of optimal fungal fruiting, but may also help in getting fungal amateurs involved in circumscribing novel species as meaningful entities in ecological and trait-based terms (Halme et al., 2012; Barron et al., 2015). While fungal amateurs mainly have a pronounced interest in finding and identifying species in the field, professional mycologists increasingly base their research on molecular tools (e.g. Horton and Bruns, 2001). However, professional mycologists could also gain clear benefits from more structured collaborations with amateurs in circumscribing fungal biodiversity. An increasingly high number of fungal species are only known from environmental sequence data, and hence cannot be described scientifically even if widely occurring in natural ecosystems (Nilsson et al., 2016). Projects that combine citizen science and barcoding could lead to these species being described and discovered as complete organisms that can be understood not only as cryptic ghosts, but also in terms of their biologically relevant traits.

For the amateurs, the importance of contributing with data to research and conservation should not be underestimated, and in this context personal experiences with finding new or very rare species are very important. It is clear from our conversations with volunteers that experiences with finding new species to Denmark have led to a deeper interest in nature and mycology, which has been shared with family, friends and landowners, further expanding the appreciation of fungi as fascinating and conservation relevant organisms. As a closing remark, we want to state that a project like ours requires close collaboration between amateurs and professionals, which is impossible without substantial funding and institutional support. Hence, we do not suggest citizen science as a cheap way to gain scientific insights, but as an important supplement to more traditional approaches that may yield larger overall benefits to science and society.

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