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Opinion Article

The next generation fungal diversity researcher

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ABSTRACT

Fungi are more important to our lives than is assumed by the general public. They can comprise both devastating pathogens and plant-associated mutualists in nature, and several species have also become important workhorses of biotechnology. Fungal diversity research has in a short time transcended from a low-tech research area to a method-intensive high-tech discipline. With the advent of the new genomic and post-genomic methodologies, large quantities of new fungal data are currently becoming available each year. Whilst these new data and methodologies may help modern fungal diversity researchers to explore and discover the yet hidden diversity within a context of biological processes and organismal diversity, they need to be reconciled with the traditional approaches. Such a synthesis is actually difficult to accomplish given the current discouraging situation of fungal biology education, especially in the areas of biodiversity and taxonomic research. The number of fungal diversity researchers and taxonomists in academic institutions is decreasing, as are opportunities for mycological education in international curricula. How can we educate and stimulate students to pursue a career in fungal diversity research and taxonomy and avoid the situation whereby only those few institutions with strong financial support are able to conduct excellent research? Our short answer is that we need a combination of increased specialization and increased collaboration, i.e. that scientists with specialized expertise (e.g., in data generation, compilation, interpretation, and communication) consistently work together to generate and deliver

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new fungal knowledge in a more integrative manner – closing the gap between both traditional and modern approaches and academic and non-academic environments. Here we discuss how this perspective could be implemented in the training of the 'next generation fungal diversity researcher'.

1. Fungi and their importance

Fungi are ubiquitous and essential components of all ecosystems on earth. Saprotrophic fungi are among the major nutrient recyclers (Boddy *et al.*, 2007). Mycorrhizal fungi have crucial impacts on terrestrial ecosystems through their symbiosis with higher plants, enhancing photosynthesis as well as the host plant's water and nutrient uptake (Smith and Read, 2008). Endophytic fungi, growing symptomless inside plants, have diverse beneficial effects to their hosts (Rodriguez *et al.*, 2009). In general, fungi directly and indirectly support human welfare through provision of diverse ecosystem services (Stajich *et al.*, 2009). In addition to the many 'do-gooders', an extremely diverse group of parasitic and pathogenic fungi can have devastating impacts on the ecosystem. Whilst fungi provide a myriad of medicines and food products, they also comprise species responsible for spoilage of food and materials, and represent direct threats to human health (Meyer *et al.*, 2016). Despite their importance to the environment and our lives (Fig. 1), the vast majority (>95 %) of fungal diversity remains undetected and much of the detected fraction lacks scientific names (Hibbett *et al.*, 2016). This applies to different levels, including yet undiscovered deep lineages of fungi as well as cryptic diversity within species (Lücking *et al.*, 2014) or even among genetically uniform individuals within a single strain (Hewitt *et al.*, 2016).

Major gaps in our knowledge of fungal diversity place us in a difficult situation as we face growing environmental challenges. Climate change, for example, is expected to have an extensive impact in natural ecosystems with direct consequences in the poorly understood mycota and increased threats from fungi habitat loss (Ainsworth *et al.*, 2015). While known and already named species can become subjects of red lists and conservation efforts, a vast diversity of unknown fungi could go extinct without notice. Other fungi may increase in abundance with unsolicited consequences, such as emerging fungal diseases of plants and animals (Garcia-Solache and Casadevall, 2010; Fisher *et al.*, 2012; Lorch *et al.*, 2016), or disruptions of food supply chains by fungal spoilage (Chakrabotry and Newton, 2011). Health problems can escalate rapidly. Fungal pathogens are currently causing more deaths than drug-resistant tuberculosis and malaria (Barnes and Rautemaa-Richardson, 2014; Calderone *et al.*, 2014; Denning and Broomley, 2015) and are prevalent in the chronic-wound microbiome (Kalan *et al.*, 2016). Environmental change will certainly also affect symbiotic systems that maintain ecosystem stability, such as mycorrhizal fungal associations or endophytes (Kivlin *et al.*, 2013; Treseder *et al.*, 2016), and even lichen-dominated habitats (Ellis and Yahr, 2011).

Given the importance of fungi, it is surprising to see a decline in mycological education and general emphasis on fungal diversity research and taxonomy at academic institutions. Experts in "phenotype-based" fungal taxonomy and systematics (i.e. those few that can recognize fungal species without DNA sequencing) are becoming a threatened race (Buyck, 1999). Fortunately, this knowledge is maintained to some extent among amateurs. At most universities, fungal biology represents only a small component of the overall academic training. Bachelor degree courses in fungal biology are rare, and mycology is often only a part of botany or microbiology courses and degrees. Mycology started out as an obscure sub-discipline of botany and although we realised long ago that plants and fungi are distantly related, in many ways mycology has continued to live in the shadow of plant science. In this environment, fungal biology teachers are underexposed to society, except in a few institutions. Too often, fungal diversity researchers and taxonomists have a limited domain of action, reduced to the dimensions of the so-called academic ivory towers. In contrast with a clear regression in fungal biology education, the field of fungal research is thriving in many aspects, as exemplified below.

In this opinion paper, we provide a summary of historic and current challenges and prospects in fungal diversity research and taxonomy, and put forward some suggestions for how the next generation fungal diversity researcher should be trained and work most effectively to fulfil the future needs of society.

2. Challenges and prospects of working with fungi

A very basic reason for the large gaps in our knowledge of fungi is that most fungi spend the majority of their life cycle belowground or within other substrates in their microbial phase, invisible to the naked eye. Moreover, a large proportion of fungi, especially in the early diverging branches of the fungal tree of life, do not produce macroscopic fruit bodies or fruit bodies at all. In the pre-DNA era, most knowledge about fungal diversity and ecology was acquired by recording and examining reproductive structures using imaging techniques (e.g., light and electron microscopy). In the second half of the last century, chemical profiling and various culture-based techniques (including mating studies and vegetative incompatibility tests), became more important. These techniques continue to provide relevant phenotypic and physiological information about fungal diversity, however, their use remains limited to fungi with macroscopically and microscopically diagnosable features or those able to grow *in vitro*.

With the introduction of PCR and Sanger sequencing techniques in the early 1990s, genetic tools made it possible to study fungi beyond the classic methodologies. Approaching

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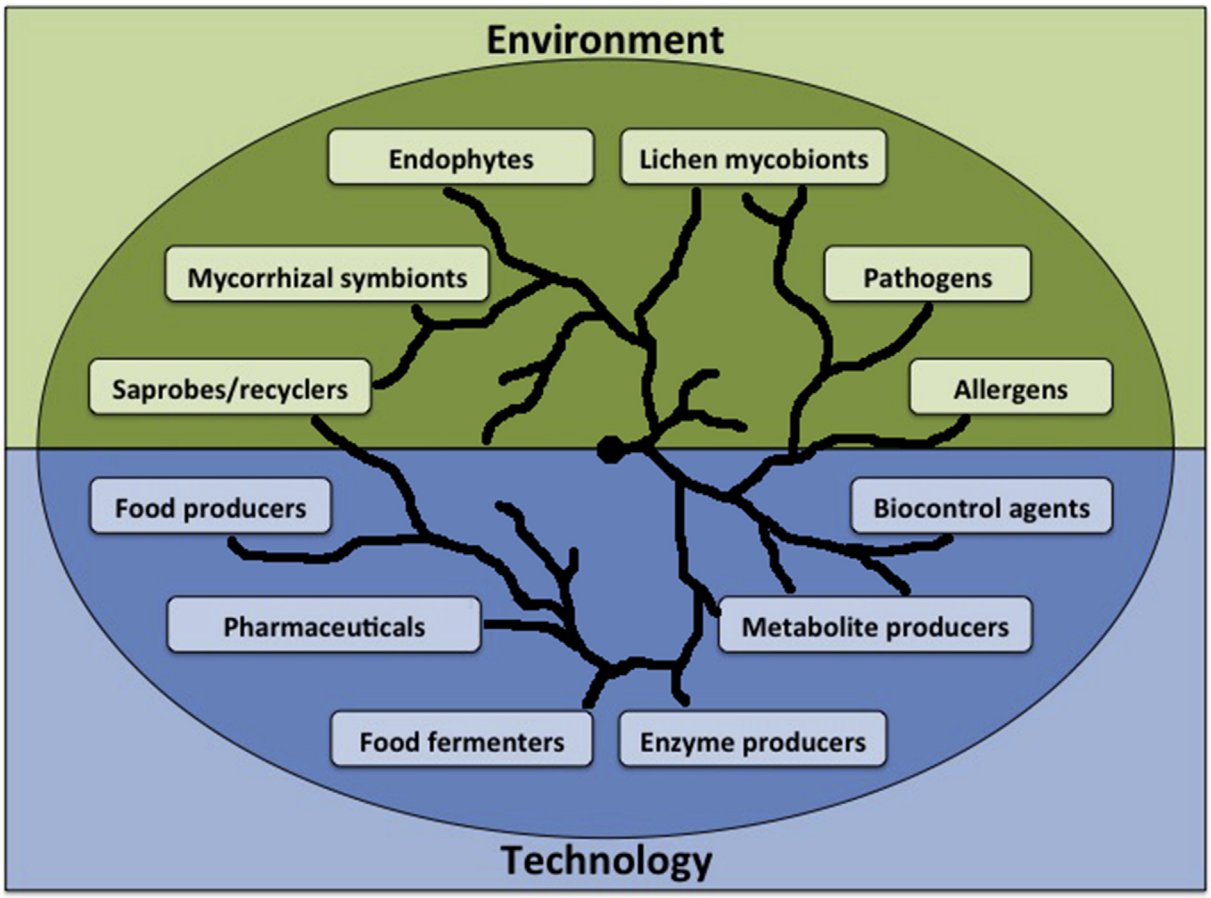

Fig. 1 – Important roles of fungi in environment and technology.

2010, another revolution in fungal diversity research took place with the introduction of high throughput sequencing (HTS) methods. These rapidly evolving HTS techniques are currently enabling a far more comprehensive (yet often biased) overview of the overall fungal diversity in environmental samples (Lindahl *et al.*, 2013). Facilitated by large and successful collaborative projects such as the 1000 Fungal Genome (1KFG) project (Grigoriev *et al.*, 2013) and other synergistic initiatives (e.g. Galagan *et al.*, 2003, 2005; Pel *et al.*, 2007; Amselem *et al.*, 2011), HTS is also providing full genome sequence data at an increasing pace. The new technologies have boosted the discovery of undescribed fungal diversity (e.g., Jones *et al.*, 2011; Spribille *et al.*, 2016), and we might be able to progress rapidly from the current figure of 135,000 described species (Hibbett *et al.*, 2016) towards the most widely accepted estimate of 3 million (Hawksworth, 2012). In addition, combining HTS approaches with RNA sequencing enables us to not just monitor what fungi are present but also to investigate what they are doing. New single-cell techniques may bring the next transition (Gawad *et al.*, 2016) and may circumvent several current challenges working with fungi. These techniques enable acquisition of both uncontaminated and less biased fungal DNA and RNA, including unculturable taxa. Single-cell analyses may also pave the way for multilocus or genomic environmental sequencing, making fungal community profiling far more accurate than the current single-locus, ITS-based approach, which can introduce significant bias (Tedersoo and Lindahl, 2016).

In parallel to the evolution of sequencing technologies, newly developed imaging methods can be combined with DNA-based techniques to more completely document fungal diversity, structure, and function. Advanced *in situ* imaging of fungal diversity is still in its infancy and needs to be adapted for a broader range of fungi. Application of specific probes combined with imaging approaches has so far been used only in a limited number of studies, which nevertheless has provided important baseline insights about the biology of the previously unseen fungi (Jones *et al.*, 2011; Spribille *et al.*, 2016). At the same time, life-history traits of fungi, which can be detected by a combination of such techniques, will help to understand the ecological contexts of the yet unexplored diversity in an integrated approach. This also applies to partitioning of genetically fixed variation from phenotypic (non-genotypic) diversity, i.e., adaptive responses or bet-hedging *vs* acclimatization (Hewitt *et al.*, 2016).

With the advent of the new technologies described above, the emergence of mainly DNA-based insights about fungal diversity have led to additional challenges and heated debates, particularly with regard to the naming of species (Hibbett and Taylor, 2013; Money, 2013; Hibbett *et al.*, 2016). A major

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caveat of HTS technology is that it produces overwhelming amounts of data, most of which remains unidentified to species or even higher taxonomic levels (Hibbett et al., 2016; Yahr et al., 2016). Moreover, a large part of the fungal kingdom cannot be documented by physical specimens as type material. Members of Cryptomycota (Jones et al., 2011; James et al., 2013), Archaeorhizomycetes (Rosling et al., 2011) and Cyphobasidiales (Spribille et al., 2016) are examples of recently detected lineages primarily documented through DNA or RNA analyses. In the current scenario, old names that could be considered potential synonyms need to be revised and formally described in accordance with the International Code of Nomenclature for Algae, Fungi and Plants (http://www.iapt-taxon.org/nomen/main.php; McNeill et al., 2012), a procedure that still requires a physical type specimen. There are, however, proposals to modify the code so as to allow sequence-based types in fungi when using environmental sequencing techniques (Hawksworth et al., 2016). De Beer et al. (2016) provides an example of successful use of environmental nucleic acid sequences (ENAS) to describe new taxa in a phylogenetic context.

In addition to the important taxonomic issues related to the hidden diversity, it is also critical that the ecological dimensions of fungi are explored. Traditionally, fungal taxonomy and ecology have been taught separately and followed separate parallel research paths. The community broadly uses other fields outside fungal biology (e.g. bioinformatics, statistics, big-data visualization), but their importance is often neither acknowledged nor included in the formal training. We wonder if the failure to integrate other fields in the mycological education has left aspiring fungal biologists unprepared to carry out top-level research and unqualified to take life science jobs.

Aside from the challenges and controversies posed above, the gains of combining various approaches and expertise to close, or at least reduce, the gap between the known and the unknown in fungal diversity is widely accepted. There are, however, daunting challenges associated with combining and complementing data from various sources and of different nature (molecular, ecological, taxonomical, morphological, distributional, functional, etc.). Synthesizing large datasets of different quality, format and completion is not a straightforward task and requires new solutions. Fungal diversity research needs to adopt data science methodologies for compiling and interpreting data. Fortunately, some efforts are emerging to solve the problem of uniting fragmented data, which include databases providing online methods for DNA sequence-based fungal identification (Kõljalg et al., 2005; Abarenkov et al., 2010; Tedersoo et al., 2015). In order to overcome the challenges related to big data interpretation, we need sophisticated visualization techniques to perceive multidimensional information. These techniques will also facilitate the communication of fungal information to scientific peers, decision makers, and the public.

3. The next generation fungal diversity researcher

The summary above reminds us that, in a few years, fungal diversity research has transcended in many ways from a low-tech research area to a methods-intensive, high-tech discipline, whilst the training of fungal diversity researchers has simultaneously reduced. Until recently, an individual researcher would typically possess the competences required to carry out state-of-the art analyses in fungal taxonomy and diversity research. Large, pan-national projects on genome sequencing of economically important fungal species have already been examples for multiauthored efforts (e.g., Galagan et al., 2003, 2005; Pel et al., 2007; Amselem et al., 2011). Recent influential studies show that major aspects of fungal diversity research are becoming highly multi-technological endeavours, as well. They integrate an array of advanced techniques and expertise such as imaging, genomics, transcriptomics, isotope analyses, modelling, and advanced statistics (Jones et al., 2011; Rosling et al., 2011; Clemmensen et al., 2013; Tedersoo et al., 2014; Spatafora et al., 2016; Spribille et al., 2016).

In this context, how can we educate the future fungal diversity researcher in a multi-technological era? How can we stimulate her/him to pursue a career in this field? And, how can we avoid a situation where only those few institutions with strong financial support are able to conduct world-class fungal diversity research? Our short answer to these questions is: through a combination of increased specialization and increased collaboration. Since most students, researchers and even research groups will clearly not have the capacity and resources to accumulate all the required skills, increased levels of national and international networking and collaboration will be essential, across both the academic and the non-academic sectors. As pointed out by Meyer et al. (2016), we live in an era where the largest portion of knowledge and capabilities related to fungal biology in general is held by industry more than academia, and we have a problem with transparency (open data) that needs to be addressed. Examples of successful collaborations between academic and industrial members can already be found in neighbouring fields, such as the multidisciplinary virtual center on fungal biotechnology – the EUROFUNG network (Meyer et al., 2016). Our approach suggested here, focused on fungal diversity and taxonomy, would represent a complementary initiative to the EUROFUNG network. Clearly, more areas of fungal research would gain from similar efforts as well.

We recognize a general workflow in modern fungal biodiversity projects (Fig. 2). This starts with data generation and subsequent compilation of data from different sources, followed by data interpretation and ultimately communication of results. For data to flow efficiently, we need better solutions to ensure that all methodological approaches remain coherent. We anticipate that next-generation fungal scientists will need to frame themselves along this conceptual pipeline, being specialized in one or a few required roles, and having a general understanding of the entire workflow. The workflow ends with science communication, a field with high potential for further development (see e.g., Nisbet and Scheufele, 2009) and that has been a commonly undervalued expertise in training programs. The next generation researchers need to communicate effectively with target groups, such as the scientific community (incl. students of biology), the public, industry and various stakeholders, to ensure knowledge exchange and to stimulate participation and engagement.

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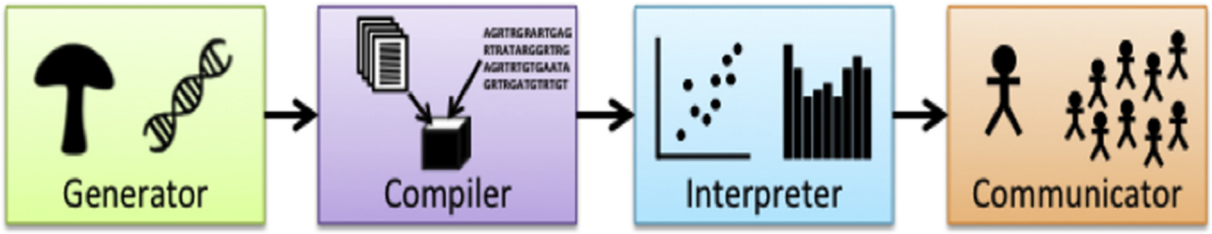

Fig. 2 – The roles of researchers in modern fungal biology.

4. Conclusion

Certainly, the application of high-end technology and the downstream data integration requires outstandingly skilled researchers. Does the training of fungal diversity researchers, as of today, cope with the needs of our time? We are very doubtful. To improve scientific excellence in fungal research, we need to be more efficient in combining 'traditional' expertise with modern technologies. Currently, only a handful of centres specialize in fungi and are able to provide adequate doctoral education for the next generation fungal diversity researchers. We argue here that the training needed can be achieved by developing a network at the level of doctoral training programs. By joining efforts from diverse scientific backgrounds and skill strengths, these heavily needed training networks may extend modern fungal diversity education more widely. Only by creating such networks will reduce the current gap between academic and non-academic institutions. The timing is right, as network schemes for postgraduate training are now feasible with the advent of national, EU and other funding initiatives for multi-student training schools. This approach could create critical masses of enthusiastic and innovative young scientists able to harness their specialist skills for effective collaboration in modern fungal research. To achieve optimal relevance, future PhDs in fungal diversity research should receive training in the data-flow pipeline outlined above. This approach will have an added benefit for those who want to enter industrial research. These young scientists will be equipped with the required expertise to quickly progress in an R&D environment that often relies on both the leverage of specific expertise and the ability to effectively connect with other disciplines. With this concept in mind, a new generation of researchers will be able to bring much needed clarity to the complex picture of fungal life and diversity. Facing an era of rapid environmental changes, we need such clarity for the wider recognition of fungi as linchpins that can determine life and death, or proliferation and decay, in all ecosystems.

REFERENCES

Abarenkov, K., Tedersoo, L., Nilsson, R.H., Vellak, K., Saar, I., Veldre, V., Parmasto, E., Prous, M., Aan, A., Ots, M., Kurina, O., Ostonen, I., Jõgeva, J., Halapuu, S., Põldmaa, K., Toots, M., Truu, J., Larsson, K.-H., Kõljalg, U., 2010. PlutoF—a web based workbench for ecological and taxonomic research, with an online implementation for fungal ITS sequences. Evol. Bioinform. Online 6, 189–196.

Ainsworth, A.M., Farley, D., Gainey, P., Penna, P., Suz, L.M., 2015. Invasion of the Orange Ping-Pong Bats: the rapidly changing distribution of *Favolaschia calocera*. Field Mycol. 16, 113–120.

Amselem, J., Cuomo, C.A., van Kan, J.A., Viaud, M., Benito, E.P., Couloux, A., Coutinho, P.M., de Vries, R.P., Dyer, P.S., Fillinger, S., Fournier, E., Gout, L., Hahn, M., Kohn, L., Lapalu, N., Plummer, K.M., Pradier, J.M., Quévillon, E., Sharon, A., Simon, A., ten Have, A., Tudzynski, B., Tudzynski, P., Wincker, P., Andrew, M., Anthouard, V., Beever, R.E., Beffa, R., Benoit, I., Bouzid, O., Brault, B., Chen, Z., Choquer, M., Collémare, J., Cotton, P., Danchin, E.G., Da Silva, C., Gautier, A., Giraud, C., Giraud, T., Gonzalez, C., Grossetete, S., Güldener, U., Henrissat, B., Howlett, B.J., Kodira, C., Kretschmer, M., Lappartient, A., Leroch, M., Levis, C., Mauceli, E., Neuvéglise, C., Oeser, B., Pearson, M., Poulain, J., Poussereau, N., Quesneville, H., Rascle, C., Schumacher, J., Ségurens, B., Sexton, A., Silva, E., Sirven, C., Soanes, D.M., Talbot, N.J., Templeton, M., Yandava, C., Yarden, O., Zeng, Q., Rollins, J.A., Lebrun, M.H., Dickman, M., 2011. Genomic analysis of the necrotrophic fungal pathogens *Sclerotinia sclerotiorum* and *Botrytis cinerea*. PLoS Genet. 7, e1002230. http://dx.doi.org/10.1371/journal.pgen.1002230.

Barnes, R., Rautemaa-Richardson, R., 2014. Fungi — forgotten foes. Bull. R. Coll. Pathol. 167, 161–162.

Boddy, L., Frankland, J., Van West, P., 2007. Ecology of Saprotrophic Basidiomycetes, , third ed.vol. 28. Academic Press, London.

Buyck, B., 1999. Taxonomists are an endangered species in Europe. Nature 401, 321.

Calderone, R., Sun, N., Gay-Andrieu, F., Groutas, W., Weerawarna, P., Prasad, S., Alex, D., Li, D., 2014. Antifungal drug discovery: the process and outcomes. Future Microbiol. 9, 791–805.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618.

Chakraborty, S., Newton, A.C., 2011. Climate change, plant diseases and food security: an overview. Plant Pathol. 60, 2–14.

de Beer, Z.W., Marincowitz, S., Duong, T.A., Kim, J.J., Rodrigues, A., Wingfield, M.J., 2016. Hawksworthiomyces gen. nov. (Ophiostomatales), illustrates the urgency for a decision on how to name novel taxa known only from environmental nucleic acid sequences (ENAS). Fungal Biol. 120, 1323–1340.

Denning, D.W., Broomley, M.J., 2015. How to bolster the antifungal pipeline. Science 347, 1414–1416.

Ellis, C.J., Yahr, R., 2011. An interdisciplinary review of climate change trends and uncertainties: lichen biodiversity, arctic-alpine ecosystems and habitat loss. In: Hodkinson, T.R.,

Jones, M.B., Waldren, S., Parnell, J.A.N. (Eds.), Climate Change, Ecology and Systematics. Cambridge University Press, Cambridge, pp. 457–489.

Fisher, M.C., Henk, D.A., Briggs, C.J., Brownstein, J.S., Madoff, L.C., McCraw, S.L., Gurr, S.J., 2012. Emerging fungal threats to animal, plant and ecosystem health. Nature 484, 186–194.

Galagan, J.E., Calvo, S.E., Borkovich, K.A., Selker, E.U., Read, N.D., Jaffe, D., FitzHugh, W., Ma, L.J., Smirnov, S., Purcell, S., Rehman, B., Elkins, T., Engels, R., Wang, S., Nielsen, C.B., Butler, J., Endrizzi, M., Qui, D., Ianakiev, P., Bell-Pedersen, D., Nelson, M.A., Werner-Washburne, M., Selitrennikoff, C.P., Kinsey, J.A., Braun, E.L., Zelter, A., Schulte, U., Kothe, G.O., Jedd, G., Mewes, W., Staben, C., Marcotte, E., Greenberg, D., Roy, A., Foley, K., Naylor, J., Stange-Thomann, N., Barrett, R., Gnerre, S., Kamal, M., Kamvysselis, M., Mauceli, E., Bielke, C., Rudd, S., Frishman, D., Krystofova, S., Rasmussen, C., Metzenberg, R.L., Perkins, D.D., Kroken, S., Cogoni, C., Macino, G., Catcheside, D., Li, W., Pratt, R.J., Osmani, S.A., DeSouza, C.P., Glass, L., Orbach, M.J., Berglund, J.A., Voelker, R., Yarden, O., Plamann, M., Seiler, S., Dunlap, J., Radford, A., Aramayo, R., Natvig, D.O., Alex, L.A., Mannhaupt, G., Ebbole, D.J., Freitag, M., Paulsen, I., Sachs, M.S., Lander, E.S., Nusbaum, C., Birren, B., 2003. The genome sequence of the filamentous fungus *Neurospora crassa*. Nature 422, 859–868.

Galagan, J.E., Calvo, S.E., Cuomo, C., Ma, L.J., Wortman, J.R., Batzoglou, S., Lee, S.I., Baştürkmen, M., Spevak, C.C., Clutterbuck, J., Kapitonov, V., Jurka, J., Scazzocchio, C., Farman, M., Butler, J., Purcell, S., Harris, S., Braus, G.H., Draht, O., Busch, S., D'Enfert, C., Bouchier, C., Goldman, G.H., Bell-Pedersen, D., Griffiths-Jones, S., Doonan, J.H., Yu, J., Vienken, K., Pain, A., Freitag, M., Selker, E.U., Archer, D.B., Peñalva, M.A., Oakley, B.R., Momany, M., Tanaka, T., Kumagai, T., Asai, K., Machida, M., Nierman, W.C., Denning, D.W., Caddick, M., Hynes, M., Paoletti, M., Fischer, R., Miller, B., Dyer, P., Sachs, M.S., Osmani, S.A., Birren, B.W., 2005. Sequencing of *Aspergillus nidulans* and comparative analysis with *A. fumigatus* and *A. oryzae*. Nature 438, 1105–1115.

Garcia-Solache, M.A., Casadevall, A., 2010. Global warming will bring new fungal diseases for mammals. mBio 1 e00061–10.

Gawad, C., Koh, W., Quake, S.R., 2016. Single-cell genome sequencing: current state of the science. Nat. Rev. Genet. 17, 175–188.

Grigoriev, I.V., Nikitin, R., Haridas, S., Kuo, A., Ohm, R., Otillar, R., Riley, R., Salamov, A., Zhao, X., Korzeniewski, F., Smirnova, T., Nordberg, H., Dubchak, I., Shabalov, I., 2013. MycoCosm portal: gearing up for 1000 fungal genomes. Nucleic Acids Res. 42 (D1), D699–D704.

Hawksworth, D.L., 2012. Global species numbers of fungi: are tropical studies and molecular approaches contributing to a more robust estimate? Biodivers. Conserv. 21, 2425–2433.

Hawksworth, D.L., Hibbett, D.S., Kirk, P.M., Lücking, R., 2016. Proposal to permit DNA sequence data to serve as types of names of "fungi". Taxon 65, 899–900.

Hewitt, S.K., Foster, D.S., Dyer, P.S., Avery, S.V., 2016. Phenotypic heterogeneity in fungi: importance and methodology. Fungal Biol. Rev. 30, 176–184.

Hibbett, D.S., Taylor, J.W., 2013. Fungal systematics: is a new age of enlightenment at hand. Nat. Rev. Microbiol. 11, 129–133.

Hibbett, D., Abarenkov, K., Kõljalg, U., Opik, M., Chai, B., Cole, J.R., Wang, Q., Crous, P.W., Robert, V.A.R.G., Helgason, T., Herr, J., Kirk, P., Lueschow, S., O'Donnell, K., Nilsson, H., Oono, R., Schoch, C.L., Smyth, C., Walker, D., Porras-Alfaro, A., Taylor, J.W., Geiser, D.M., 2016. Sequence-based classification and identification of fungi. Mycologia. http://dx.doi.org/10.3852/16–130.

James, T.Y., Pelin, A., Bonen, L., Arhendt, S., Sain, D., Corradi, N., Stajich, J.E., 2013. Shared signatures of parasitism and phylogenomics unite Cryptomycota and microsporidia. Curr. Biol. 23, 1548–1553.

Jones, M.D., Forn, I., Gadelha, C., Egan, M.J., Bass, D., Massana, R., Richards, T.A., 2011. Discovery of novel intermediate forms redefines the fungal tree of life. Nature 474, 200–203.

Kalan, L., Loesche, M., Hodkinson, B.P., Heilmann, K., Ruthel, G., Gardner, S.E., Grice, E.A., 2016. Redefining the chronic-wound microbiome: fungal communities are prevalent, dynamic, and associated with delayed healing. mBio 7 e01058–16.

Kivlin, S.N., Emery, S.M., Rudgers, J.A., 2013. Fungal symbionts alter plant responses to global change. Am. J. Bot. 100, 1445–1457.

Kõljalg, U., Larsson, K.H., Abarenkov, K., Nilsson, R.H., Alexander, I.J., Eberhardt, U., Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A.F., Tedersoo, L., Vrålstad, T., Ursing, B.M., 2005. UNITE: a database providing web-based methods for the molecular identification of ectomycorrhizal fungi. New Phytol. 166, 1063–1068.

Lindahl, B.D., Nilsson, R.H., Tedersoo, L., Abarenkov, K., Carlsen, T., Kjøller, R., Kõljalg, U., Pennanen, T., Rosendahl, S., Stenlid, J., Kauserud, H., 2013. Fungal community analysis by high-throughput sequencing of amplified markers – a user's guide. New Phytologist 199, 288–299. http://dx.doi.org/10.1111/nph.12243. Q3

Lorch, J.M., Palmer, J.M., Lindner, D.L., Ballmann, A.E., George, K.G., Griffin, K., Knowles, S., Huckabee, J.R., Haman, K.H., Anderson, C.D., Becker, P.A., Buchanan, J.B., Foster, J.T., Blehert, D.S., 2016. First detection of bat white-nose syndrome in western North America. mSphere 1 e00148–16.

Lücking, R., Dal-Forno, M., Sikaroodi, M., Gillevet, P.M., Bungartz, F., Moncada, B., Lawrey, J.D., 2014. A single macrolichen constitutes hundreds of unrecognized species. Proc. Natl. Acad. Sci. U. S. A. 111, 11091–11096.

McNeill, J., Barrie, F.R., Buck, W.R., DeMoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H., Turland, N.J., 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Regnum Vegetabile 154. Koeltz Scientific Books, ISBN 978-3-87429-425-6.

Meyer, V., Andersen, M.R., Brakhage, A.A., Braus, G.H., Caddick, M.X., Cairns, T.C., de Vries, R.P., Haarmann, T., Hansen, K., Hertz-Fowler, C., Krappmann, S., Mortensen, U.H., Penalva, M.A., Ram, A.F.J., Head, R.M., 2016. Current challenges of research on filamentous fungi in relation to human welfare and a sustainable bio-economy: a white paper. Fungal Biol. Biotechnol. 3, 6.

Money, N.P., 2013. Against the naming of fungi. Fungal Biol. 117, 463–465.

Nisbet, M.C., Scheufele, D.A., 2009. What's next for science communication? Promising directions and lingering distractions. Am. J. Bot. 96, 1767–1778.

Pel, H.J., de Winde, J.H., Archer, D.B., Dyer, P.S., Hofmann, G., Schaap, P.J., Turner, G., de Vries, R.P., Albang, R., Albermann, K., Andersen, M.R., Bendtsen, J.D., Benen, J.A., van den Berg, M., Breestraat, S., Caddick, M.X., Contreras, R., Cornell, M., Coutinho, P.M., Danchin, E.G., Debets, A.J., Dekker, P., van Dijck, P.W., van Dijk, A., Dijkhuizen, L., Driessen, A.J., d'Enfert, C., Geysens, S., Goosen, C., Groot, G.S., de Groot, P.W., Guillemette, T., Henrissat, B., Herweijer, M., van den Hombergh, J.P., van den Hondel, C.A., van der Heijden, R.T., van der Kaaij, R.M., Klis, F.M., Kools, H.J., Kubicek, C.P., van Kuyk, P.A., Lauber, J., Lu, X., van der Maarel, M.J., Meulenberg, R., Menke, H., Mortimer, M.A., Nielsen, J., Oliver, S.G., Olsthoorn, M., Pal, K., van Peij, N.N., Ram, A.F., Rinas, U., Roubos, J.A., Sagt, C.M., Schmoll, M., Sun, J., Ussery, D., Varga, J., Vervecken, W., van de

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Vondervoort, P.J., Wedler, H., Wösten, H.A., Zeng, A.P., van Ooyen, A.J., Visser, J., Stam, H., 2007. Genome sequencing and analysis of the versatile cell factory *Aspergillus niger* CBS 513.88. Nat. Biotechnol. 25, 221–231.

Rodriguez, R.J., White Jr., J.F., Arnold, A.E., Redman, R.S., 2009. Fungal endophytes: diversity and functional roles. New Phytol. 182, 314–330.

Rosling, A., Cox, F., Cruz-Martinez, K., Ihrmark, K., Grelet, G.-A., Lindahl, B.D., Menkis, A., James, T.Y., 2011. Archaeorhizomycetes: unearthing an ancient class of ubiquitous soil fungi. Science 333, 876–879.

Smith, S.A.A., Read, D., 2008. Mycorrhizal Symbiosis, third ed. Academic Press.

Spatafora, J.W., Chang, Y., Benny, G.L., Berbee, M.L., Bonito, G., Corradi, N., Grigoriev, I., Gryganskyi, A., James, T.Y., O'Donnell, K., Taylor, T.N., Uehling, J., Vilgalys, R., White, M.M., Stajich, J.E., 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108, 1028–1046.

Spribille, T., Tuovinen, V., Resl, P., Vanderpool, D., Wolinski, H., Aime, M.C., Mayrhofer, H., Johanneson, H., McCutcheon, J., 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. Science 353, 488–492.

Stajich, J.E., Berbee, M.L., Blackwell, M., Hibbett, D.S., James, T.Y., Spatafora, J.W., Taylor, J.W., 2009. The fungi. Curr. Biol. 19, R840–R845.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L-d., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346, 1256688.

Tedersoo, L., Ramirez, K.S., Nilsson, R.H., Kaljuvee, A., Kõljalg, U., Abarenkov, K., 2015. Standardizing metadata and taxonomic identification in metabarcoding studies. GigaScience 4, 1.

Tedersoo, L., Lindahl, B., 2016. Fungal identification biases in microbiome projects. Environ. Microbiol. Rep. 8, 772–779. http://dx.doi.org/10.1111/1758-2229.12438.

Treseder, K.K., Marusenko, Y., Romero-Olivares, A.L., Maltz, M.R., 2016. Experimental warming alters potential function of the fungal community in boreal forest. Glob. Chang. Biol. 22, 3395–3404.

Yahr, R., Schoch, C.L., Dentinger, B.T., 2016. Scaling up discovery of hidden diversity in fungi: impacts of barcoding approaches. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150336. Q4

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