Diversity and distribution of ligninolytic fungi

Associate Professor Inger Skrede, Department of Biosciences, University of Oslo, Oslo, Norway

Abstract

Ligninolytic fungi is a large and heterogeneous group of species, mainly from the two phyla Ascomycota and Basidiomycota. They are the main players in the decomposition of wooden materials worldwide. In this chapter, the diversity and distribution of ligninolytic fungal species is presented. Attention is given to how the species diversity can be detected, as fungi are mainly living within their substrate and consequently may be difficult to observe. I present the current knowledge on how the species diversity originates, and the discovery of cryptic ligninolytic fungal species. I also focus on the distribution of ligninolytic fungi, both on how individuals are locally distributed on a single substrate of dead wood and on how species are distributed at larger scales. Across larger scales fungi are affected by the size and environmental conditions in local forests and large-scale climatic variables. The chapter ends with a discussion about conservation, with some perspectives for future research directions.

Keywords: diversity, distribution, speciation, divergence, local adaptation, conservation, wood decay, DNA metabarcoding, population genetics

Contents

1. Introduction

Ligninolytic fungi are saprotrophic species decomposing dead wood. This is a large and heterogeneous group of fungi from many different fungal orders, that have evolved the ability to live on this recalcitrant material. There have been several reviews summarizing the knowledge of fungal evolution and divergence at various taxonomic levels (Giraud et al., 2008; Gladieux et al., 2014; James et al., 2020; Stukenbrock, 2013). A lot of the current knowledge is derived from fungal model organisms such as *Saccharomyces* and *Neurospora*, or plant pathogens such as *Fusarium* and *Zymoseptoria*. Nevertheless, there are constant gain of knowledge and development in the field also for non-model organisms. The development of genomic tools, allowing detailed genomic analyses of non-model organisms and DNA based diversity studies, are current drivers of new research understanding their diversity, divergence and distribution. In this chapter I aim to review the knowledge in the field of fungal diversity and distribution with the focus on ligninolytic fungi. Lignolytic fungi can be long-lived, decaying large logs and fruiting on old logs, such as *Phellopilus nigrolimitatus*. Alternatively, they can be ephemeral pioneer species, decaying only recently fallen logs or small twigs, such as *Trichaptum abietinum* and *Schizophyllum commune*. In particular, the long-lived species will put larger investments into decaying the substrate and have a very different life history than many plant pathogens and yeast species.

In this chapter I will introduce the current knowledge of diversity of ligninolytic fungi. I will discuss how to define ligninolytic fungal species, and how these species originate and diverge through speciation and hybridization. Further I will discuss why the different species are where they are, how they adapt to their environment, and the conservation needs.

2. Diversity, cryptic species and speciation

2.1 Diversity of fungi

Currently there are about 150 000 fungal species described, with 2 000 new species being described each year (Niskanen & Douglas, 2018). However, the estimated total number of fungal species in the world varies from 1.5 to 6 million (Blackwell, 2011; Hawksworth, 1991; Hawksworth & Lucking, 2017; Taylor et al., 2014; Tedersoo et al., 2014) and is thus highly uncertain. The primary cause of this uncertainty is that fungi spend most of their life cycle hidden within substrates such as soil, wood, or within other organisms and cannot easily be

observed. The different estimates of the total fungal diversity have often been based on a comparison to the better-known plant diversity. The estimate of 1.5 million fungal species was mainly based on fungus to plant ratio of 6:1 (Hawksworth, 1991). Later, Taylor *et al*. (2014) suggested that a ratio of 17:1 is more reasonable in soils from Alaska, and if this estimate should be expanded for the whole world, which would suggest 6 million fungal species. A general pattern of increasing species ranges towards higher latitude has been suggested, this implies decreasing species diversity at higher latitudes – referred to as Rapoports rule (Stevens, 1989). A global study of species diversity in soil samples indicated that most fungal species also have wider distribution towards the poles (Tedersoo et al., 2014). Although, several fungal groups have a different pattern, i.e. ectomycorrhizal fungi have higher diversity in temporal regions than in the tropics and lichens have the largest diversity in the arctic (Tedersoo et al., 2012, 2014). Hence, fungal richness estimates based solely on plant diversity can be highly insecure, as fungi may follow a different diversity patterns to other organisms.

2.2 Diversity of ligninolytic fungi

Fungi grow on and inside their substrate and the species diversity may be difficult to observe. For ligninolytic fungi, this substrate is dead wood. In the Nordic countries alone, it has been documented more than 2500 fungal species growing on dead wood (Stenlid et al., 2008; Stokland & Meyke, 2008; Stokland & Siitonen, 2012). These are mainly species that produce fruit bodies and can thus be observed and identified. Of these species, about 1600 species are basidiomycetes, and about 900 are ascomycetes. Most ligninolytic species are obligately growing on wood, but some fungal species growing on dead wood are facultative, i.e. they can grow on many different substates, with wood as one of these substrates (Stokland & Siitonen, 2012). Some fungal species are found on wood, but decay or parasitize other fungal species – called fungicolous species, and will not be treated in this chapter (see Maurice et al., 2021 for more details.

The phylum Basidiomycota includes the efficient white rot and brown rot. These are distributed in several different orders, listed here, with the examples of included genera (in parentheses), i.e. Polyporales (*Fomitopsis*, *Antrodia*, *Antrodiella*, *Datronia*, *Meruliopsis, Trametes*, *Phlebia, Phlebiopsis, Phanerochaete, Postia, Pycnoporus* and *Sistotrema*), Agaricales (*Armillaria, Schizophyllum* and *Pleurotus*), Hymenochaetales (*Trichaptum*, *Phellopilus* and *Phellinus*), Boletales (*Coniophora* and *Serpula*), and Russulales (*Heterobasidion* and *Hericium*). The ligninolytic species of Ascomycota are often less

conspicuous, but some of the well-known species are in the orders: Xylariales (*Daldinia* and *Xylaria*), Hypocreales (*Trichoderma*), Pleosporales, Sordariales (*Neurospora*) and Helotiales (*Ascocoryne* and *Bisporella*). In addition, there are many ligninolytic species found in less diverse orders throughout the Basidiomycota and Ascomycota.

Estimates of species diversity on dead wood have traditionally been based on fruit body surveys on decomposing logs. Exemplified by interesting studies of the effect the amount of dead wood has on fungal diversity (Hottola et al., 2009) and species diversity in Tasmanian woodland (Gates et al., 2011). However, there are several reasons why a species may not be detected in such surveys. Many species, especially ascomycetes, have microscopic fruit bodies which can be hard to detect. For species with ephemeral fruiting bodies, the fungus may not fruit at the time of the survey. This was especially pinpointed in Nordén *et al*. (2013), where fungi that are specialized to fruit on old decayed logs were rarely observed. In the recent years, DNA-based studies have cast further light on the diversity of ligninolytic fungi. By amplifying a specific genetic region (usually the nuclear ribosomal Internal Transcribed Spacers ITS1 or ITS2), sequencing the amplicon with a high throughput sequencing technology and matching the resulting DNA sequences with established databases, the diversity of environmental samples can be investigated – an approach called DNA metabarcoding. In 2013, Ovaskainen and colleagues investigated the diversity of fungi growing in 100 Norway spruce logs of variable decay grade by fruit body surveys and DNA metabarcoding analyses. They observed higher diversity with the DNA metabarcoding approach, than from the fruitbody surveys. Those species that are highly specialized or only fruits after several years decaying the same log were more often detected with the DNA metabarcoding approach. On the other hand, species that fruits rapidly after establishment were more commonly detected in the fruit body survey data. The low detection rate in the DNA metabarcoding data of these ephemeral species was explained by a small mycelial mass, thus they were not present in the particular sawdust samples (Ovaskainen et al., 2013). Several studies have suggested that a combination of both fruit body surveys and DNA metabarcoding may give a more complete picture of the species diversity in a log (Ottosson et al., 2015; Ovaskainen et al., 2013; Saine et al., 2020). Another option is to include many DNA metabarcoding samples from each log in order to register the diversity in the heterogeneous woody substrate. Recent DNA metabarcoding studies have shown that species known to fruit in late decay stages were also present in earlier decay stages of oak, fir and spruce logs (Baldrian et al., 2016) and that they are possibly also present for a long time after fruiting, as shown in Norwegian spruce logs (Ottosson et al., 2015).

The units detected by DNA metabarcoding studies cannot be directly compared to species and are referred to as operational taxonomic units (OTUs). Sometimes the sequences from several species can be combined into one OTU, or intraspecific variation may split sequences from one species into several OTUs (Blaalid et al., 2013; Nilsson et al., 2008). Two OTUs were found within each of the two species *Phellopilus nigrolimitatus* and *Phlebia centrifuga* including 16 fruit bodies from one location (Estensmo et al., 2021). Thus, fungal richness from DNA metabarcoding data cannot be directly extrapolated as species richness. This leads us to the question of "what are species?" that will be discussed in the next section.

2.3 Fungal divergence and cryptic species

Species concepts have caused lot of controversy over the years (Wheeler and Meier, 2000). As scientists have used different species concepts and criteria to define species in their favorite organisms, it has been impossible to agree on one single definition of species. In this chapter I will not discuss the number of species concepts that have been proposed, or claim that one is better than others, however, I will focus on the criteria that are practically used in the mycological community to distinguish species. Further, I will discuss what we currently know and do not know about species divergence.

Historically, the morphological species concept was the most commonly applied concept in fungal studies. The species concept uses macroscopic and microscopic morphological characters to define and distinguish different species. This concept is practical and can often be used to identify species in the field. However, ligninolytic fungi often have few morphological characters, mostly related to fruit body traits, and as discussed previously, they often live most of their life within their substrate. Thus, during the last 30 years, it has become clear that many of the morphological characters that are used to distinguish species are not necessarily recognizing species as independent evolutionary units nor inform about the relationship among species.

After molecular markers became available for the mycological research community, the phylogenetic and the genealogical concordance phylogenetic species recognition (GCPSR) approach have been well received (Dettman, Jacobson, & Taylor, 2003; Dettman, Jacobson, Turner, et al., 2003; Liti et al., 2006; Taylor et al., 2000). The phylogenetic species concept uses phylogenetic relationships to define monophyletic groups as species. This was further developed in the GCPSR, and the criteria are that more than one genetic region should support

the monophyletic group, and that no other genetic region should be incongruent with this group. Using molecular markers to enlighten the phylogenetic relationships and evolutionary units in fungi, have further guided which morphological characters that can be used to distinguish species defined by the GCPSR. Thus, the morphology is still relevant, but it is a matter of knowing which morphological characters to use.

Other species concepts are more mechanistic, such as the biological species concept. The criteria of the biological species concept are that the individuals within a species are reproductively compatible and the progeny is fertile. Thus, in order to test the criteria for this species concept for fungi, they need to be sexual organism. The implication of an asexual reproductive life cycle is discussed further down, but a purely asexual life cycle is not as common in fungi as previously thought (Taylor et al., 2015). Further, we need to be able to observe mating or the products of mating.

The evolutionary units that currently exist in nature is not always easy to observe. Cryptic species are morphologically indiscernible, but genetic distinct, reproductive isolated lineages. After the development of molecular markers to test species relationships, several cryptic ligninolytic species have been found within fungal morphospecies. The difficulty in distinguishing species morphologically contributes to the uncertainty of the current fungal species richness estimates.

The *Heterobasidion annosum* species complex (*H. annosum sensu lato*) is the most destructive forest pathogen in the Northern Hemisphere, and can almost be considered a model for cryptic speciation in wood decay species. In this complex there are three species in Europe (*H. parviporum*, *H. abietinum* and *H. annosum sensu stricto*) and two species in North America (*H. occidentale* and *H. irregulare*), that previously were considered to be one species (*H. annosum s.l.*) (Dalman et al., 2010; Garbelotto et al., 1998, 2007; Johannesson & Stenlid, 2003). These five species are divided into two main clades, one clade with *H. abietinum*, *H. parviporum* and *H. occidentale* and another clade with *H. irregulare* and *H. annosum* s. s. (Dalman et al., 2010). The split between these two clades was dated to about 60 Mya ago (Dalman et al., 2010). Thus, an old event has led to diversification in this species complex and the two clades have co-existed for millions of years.

Trichaptum abietinum is a pioneer species that rapidly produce small fruit bodies on recently fallen spruce logs all over the temporal and boreal region. In crossing experiment of individuals from North America, Macrae (1967) and Magasi (1976) found two sympatric, morphological inseparable, reproductively isolated populations. A recent study revealed that

these reproductively isolated populations of *T. abietinum* probably are genetically divergent (Seierstad et al., 2020), which supports that these are different evolutionary units. Likewise, intersterility groups were found within the morphologically defined species *Armillaria mellea* (Anderson et al., 1980; Anderson & Ullrich, 1979) and *Fomitopsis pinicola* (Mounce & Macrae, 1938) in North America. Also, for *F. pinicola*, two sympatric genetic groups were revealed, when revisiting the reproductive isolated groups in the widespread morphospecies (this time with molecular markers, Haight et al., 2016). Previously, no population structure was detected within Europe for *F. pinicola* (Högberg et al., 1999).

Phylogenetic studies have revealed cryptic species in many genera of wood decay fungi. Five cryptic species were detected within the morphospecies complex of *Serpula himantioides* (Carlsen et al., 2011). One of these cryptic species was spanning temporal regions worldwide, decaying varying substrates in forests (mostly gymnosperm wood) and houses. The other *S. himantioides* lineages had narrower distribution ranges, including one restricted to South America, here found in the built environment and on *Nothofagus* dead wood in nature (Carlsen et al., 2011). Several cryptic species have also been detected within the three *Coniophora* morphospecies *C. puteana*, *C. olivacea* and *C. arida* (Kauserud, Shalchian-Tabrizi, et al., 2007; Kauserud, Svegarden, Decock, et al., 2007; Skrede et al., 2012).

Cryptic species are also found in ligninolytic ascomycetes. In the genus *Daldinia*, five species were found in Europe, where three of these previously was referred to as *D. concentrica* (Johannesson et al., 2000). Further, eight species were found within the genus *Neurospora* where five corresponded to defined morphospecies, and three were newly defined using molecular data and phylogenetic analyses (Dettman, Jacobson, & Taylor, 2003).

All the cryptic species discussed above have been distinguished by a variety of molecular markers, also those that were first distinguished by reproductive barriers. How many markers and which ones are needed to distinguish species vary from group to group. In the *Hypholoma fasciculare* complex, it was shown that many molecular markers and phylogenetic tools were needed to recognize cryptic species within this species complex (Sato et al., 2020). While in the *Serpulaceae* it was shown that it is not the number of markers that is important *per se*, but selecting a few and informative markers (Balasundaram et al., 2015). Which molecular markers that have evolved in an even rate and are presenting the history of species divergence will vary from clade to clade and should thus be evaluated for each study.

2.4 Speciation mechanisms in ligninolytic fungi

Even if many fungal species are known, and the estimated species diversity is high, little is known about how they originate and undergo speciation. In this section I will focus on speciation mechanisms in ligninolytic basidiomycete fungi, and present some possibilities for future research.

Most ligninolytic basidiomycete fungi spend most of their life cycle as dikaryotic mycelia. However, some exceptions are known, where the mycelia contain multiple nuclei, e.g. in *Heterobasidion parviporum*, imbalanced nuclear ratios between multiple nuclei may exist (James et al., 2008). The fusion of the two nuclei into a diploid zygote that undergoes meiosis, happens in the hymenium of the fruit bodies. Hence, the plasmogamy (fusion of cytoplasm) and karyogamy (fusion of nuclei) can be separated in time for years, which seems to be a unique feature for basidiomycetes. A common procedure to investigate reproductive barriers in Basidiomycota has been to assess whether dikaryotic mycelia are formed when monokaryotic mycelia are crossed *in vitro*, as was done for *T. abietinum. F. pinicola* and *A. mellea* to distinguish the sympatric reproductively groups in North America (Anderson et al., 1980; Anderson & Ullrich, 1979; Macrae, 1967; Magasi, 1976; Mounce & Macrae, 1938). However, even if the dikaryotization process is well characterized (i.e. see Anderson & Kohn, 2007), it only represents the first step towards mating. Thus, successful dikaryotization is not synonymous with reproductive success.

Successful reproduction following crosses between differentiated populations may depend on ecological factors that prevent different populations from mating; as residing in different geographic regions, fruiting in different seasons or growing on different substrates. Further, genes that preclude plasmogamy, fruitbody formation or karyogamy will also restrict mating between populations. If the individuals can mate, there may still be mechanisms that prevent successful reproduction as hybrid sterility or inviability that could be caused by either ecological factors or genomic incompatibility. For example, a hybrid diploid might encounter problems during meiosis due to chromosomal rearrangements, resulting in a failure of haploid spore production or in spores that are less adapted to germinate in the local environment.

Such reproductive barriers may shape patterns of genomic differentiation observed among fungal lineages. If reproductive barriers are complete (or if speciation has occurred in allopatry), then genome-wide differentiation is predicted, with some heterogeneity due to the effects of selection and variation in rates of mutation and recombination. Greater genomic

heterogeneity is expected when reproductive barriers are incomplete and divergence is maintained in the presence of gene flow. For example, patchy divergence (e.g. genomic islands of divergence) has been reported in the ascomycete species *Neurospora crassa* where adaptation to ecologically different features appears to have enhanced divergence (Ellison et al., 2011). Further, studies of fungal plant pathogens have suggested that genome rearrangements could be an especially important speciation mechanism for fungi (Plissonneau et al., 2016; Raffaele & Kamoun, 2012; Stukenbrock, 2013). The role of genome rearrangements should be further evaluated for ligninolytic fungi.

The nature of reproductive isolation also affects the outcomes of hybridization. If reproductive barriers are weak or incomplete, some hybrid genotypes may be as fit as the parents, or even more fit. In such a scenario, the parental lineages may fuse back into a single species (reverse speciation), or produce a third species (hybrid speciation). Hybrid speciation has been reported for many different organisms, and it has been shown for the fungal pathogen *Zymoseptoria* (Stukenbrock et al., 2012) and recurrently in the true yeast of *Saccharomyces*. In *Saccharomyces*, that are often found on living trees in nature, but may not be defined as ligninolytic fungi, hybridization and polyploidization have led to the origin of many new species (Eberlein et al., 2019; Langdon et al., 2019; Libkind et al., 2011; Peris et al., 2016). Some of these species have been domesticated for fermentation properties, or after the initial domestication process as *S. pastorianus* which probably hybridized in the human habitat (Dunn & Sherlock, 2008).

If reproductive barriers are strong and genetically complex, essentially all hybrids will be less fit than their parents as they will have less chances of finding a mate. In this case, it will be advantageous to produce offspring possessing stronger pre-zygotic barriers to prevent maladaptive hybridization. This may lead to the strengthening or 'reinforcement' of reproductive barriers (Dobzhansky, 1937). While the importance of reinforcement was questioned by early theoretical papers, there is empirical evidence for this process for many organisms e.g. flies (Ortiz-Barrientos et al., 2004; Servedio & Noor, 2003), birds (Sætre et al., 1997), plants (Hopkins, 2013) and for *Neurospora* (Dettman et al., 2008; Dettman, Jacobson, Turner, et al., 2003) and *H. annosum s.l.* (Garbelotto et al., 2007; Olson & Stenlid, 2001). In *Neurospora*, specific loci related to reinforcement were detected for prezygotic, post mating reproductive barriers (Turner et al., 2011). In *H. annosum s.l.* the reinforcement could support the origin of substrate specialization as hybrids were less fit on specific substrates (Garbelotto et al., 2007). Reinforcement could also explain the patterns of reproductive isolation found

among sympatric groups in *T. abietinum* and *F. pinicola*.

Although knowledge on fungal speciation mechanisms is emerging from some model systems, recent review papers have pinpointed the lack of knowledge on speciation processes in non-model fungi (Giraud et al., 2008; Gladieux et al., 2014; Stukenbrock, 2013). The temporal separation of plasmogamy and karyogamy in most ligninolytic basidiomycetes may lead to distinct evolutionary dynamics and genome organization as the two haploid nuclei can evolve independently until karyogamy (Anderson & Kohn, 2007). In some species it has also been suggested that the nuclei can go through mitotic recombination during their dikaryotic stage, a process known as parasexuality (Nieuwenhuis & James, 2016) or mate recurrently by transferring one nuclei from a dikaryon to a new monokaryon to form a dikaryon with a new nucleic combination. In the future, ligninolytic wood decay fungi should be ideal organisms to study speciation processes due to the small genomes of these fungi (average of basidiomycetes is 46.5 Mb (Mohanta & Bae, 2015)), which allows for a detailed investigation of the role of chromosomal reorganization, genomic islands of divergence and selection of specific genes during speciation. Further, they are often culturable, which allows *in vitro* experiments evaluating pre- and postzygotic barriers. To understand how these organisms evolve, is of major importance to understand the emergence of ligninolytic fungal species with important ecosystem functions.

3. Individuality and population divergence

As with other organisms, wood decay fungi consist of species, with populations of individuals. In this section, fungal individuality, how the individuals are distributed in the landscape and the gene flow among these individuals and among populations will be discussed.

3.1 Individuality

Fungi are modular organisms. Compared to most animals and plants that have more defined body size and limits, it is more difficult to observe where a fungal body starts and ends. Filamentous fungi have hyphae that can grow in different directions, and that may produce fruit bodies from different parts of the mycelium. Thus, different fruit bodies on a single log may represent the same or different mycelial individuals. Fungi recognize self from non-self, using vegetative incompatibility loci (vic or het). If mycelia have different alleles at these loci, they

will recognize each other as non-self, and usually a confrontation zone is formed. This can sometimes be observed as black lines in the decayed wood. These confrontation lines have also been used to test *in vitro*, if mycelia collected at different sites are different individuals. The two different mycelia are then placed in one petri dish, and whether a confrontation zone is formed can be visually observed. The confrontation zone is formed to avoid mixing of genotypes, to defend the substrate, and possibly also to avoid infections (reviewed by Paoletti, 2016).

Most ligninolytic fungi disperse from one log to the next through air by sexual spores. The spores will usually establish on the logs as monokaryons that mate with a compatible spore or another monokaryon. When the mating happens depend on the fungal group, ascomycetes mate just before fruitbody formation, while basidiomycetes mainly live as dikaryons until fruiting. For most species, fruit bodies on different logs would then represent different individuals. However, there are some interesting cases where an individual can spread from one log to the next by mycelial growth and not only by spores. It has been shown that *Armillaria* can spread over extreme distances with rhizomorphs (Anderson et al., 2018; Ferguson et al., 2003; Smith et al., 1992). By using confrontation experiments, one individual of *Armillaria ostroyae* in Oregon, USA, spanning 965 hectares (3.8 km in diameter) was found, which is the largest known organism on earth (Ferguson et al., 2003). *Armillaria* is both pathogenic and a wood decay fungus, and has by the occurrence of some large individuals been popularly referred to as "the humongous fungus". Even if a few *Armillaria* individuals spread out to reach huge sizes, most individuals obtain smaller sizes (Anderson et al., 2018). An even more complex issue of fungal individuality is the ability of some species to mate recurrently, as was briefly mentioned in the previous section. In *T. abietinum,* 82% of all monokaryons that were paired with a dikaryon resulted in a dikaryotic strain (Kauserud & Schumacher, 2003b). Thus, a nucleus from a dikaryotic mycelium can be transferred to a new monokaryon and form another dikaryon, known as Bullers phenomenon or di-mon mating (Buller, 1930; Snider & Raper, 1958). This has been investigated in detail in *Schizophyllum commune* (Crowe, 1960; Ellingboe & Raper, 1962; Nieuwenhuis et al., 2011), but is also known from other ligninolytic species e.g. *Pholiota nameko* (Nogami et al., 2002) and *Armilllaria gallica* (Carvalho et al., 1995), and may be a common phenomenon in ligninolytic fungi.

It was previously thought that many fungi were asexual. However molecular data and genome sequencing have revealed that many of these clonal fungi, actually have a "cryptic" sexual stage. For some species, the morphology of the sexual and asexual structures is very

different and thus these structures were not recognized as the same species. For example, the early season asexual structures and the late season sexual structures created taxonomic confusion in the widespread species *Xylaria hypoxylon* and *Ascocoryne sarcoides* (see photos of the asexual and sexual structures of *A. sarcoides* in Figure 1). Even if the ability to produce both asexual and sexual structures and spores are most common in ascomycetes it also occurs in basidiomycetes, e.g. in *Postia ptychogaster* (Ryvarden & Gilbertson, 1994). Thus, fungi, and especially ascomycetes, are flexible by having the ability to shift between asexual and sexual stages when this is advantageous. However, very few species can be considered purely asexual (J. W. Taylor et al., 2015). To my knowledge, no purely asexual basidiomycete ligninolytic fungi are known, even if self-fertilization (homothallism) is known in e.g. *Sistotrema brinkmannii* (Ullrich & Raper, 1975) and *Armillaria mellea* (Baumgartner et al., 2012), and within several genera in the Hymenochaetales (Rajchenberg, 2011). More investigations are needed to test whether these findings are mostly due to the lack of clamp formation in the dikaryons formed, which makes mating difficult to observe.

It is common that several individuals of the same species grow on the same log. This was the case of *T. abietinum* when cultures made from different fruitbodies found the same log were confronted with each other – almost all fruitbodies were different individuals (Kauserud & Schumacher, 2003b). Fewer fruit bodies were found in the rare, and in some countries, redlisted, pocket rot species *Phellopilus nigrolimitatus.* This species is known to produce fruit bodies on heavily decayed logs, but it may be present in the log for a long period before it fruits (Ovaskainen et al., 2013). From 42 cultures produced from fruit bodies and sawdust of three logs, 7 individuals could be detected (Kauserud & Schumacher, 2002). This has recently been revisited, where 53 different individuals were identified among 230 dikaryotic isolates of *P. nigrolimitatus*, distributed on 6 logs, where 6 to 12 individuals were found on each log (Jensen et al., 2020). On the contrary, only a single individual of *Serpula lacrymans* (known to decay wood in the built environment) is usually found in each house (Bjørnaraa, 2013).

3.2 Population size, divergence and gene flow within ligninolytic species

Populations sizes of ligninolytic fungi varies from species living in small, defined, endemic populations to species that are widespread, and where the divergence is probably more driven by isolation by distance than distinct population structure. Thus, for some species it may be difficult to define specific populations and population sizes.

This is the case for the widely distributed and abundant white rot decay fungus *Schizophyllum commune*. This species possesses extremely high genetic diversity (nucleic acid diversity of 0.20 in the US population was observed) as was shown by full genome sequencing of individuals from USA and Russia (Baranova et al., 2015). There are several possible explanations to this, and the authors argued that it is mostly due to high mutation rate, and partially due to large population sizes. Individuals from the two continents were divergent, but little divergence was observed within continents, as also supported by previous studies suggesting that intercontinental long-distance dispersal and gene flow is rare (James et al., 1999; James & Vilgalys, 2001).

Even closely related species may have very different divergence and dispersal rates. In the two sister species *Trichaptum fuscoviolaceum* and *T. abietinum* the population sizes and divergence seem to differ. In *T. abietinum* there is several reproductively isolated groups, as was discussed in section 2, while in *T. fusocviolaceum* there seem to be two more closely related populations and no observed reproductive barriers (Kauserud & Schumacher, 2003c; Macrae, 1967; Seierstad et al., 2020).

Within the Fennoscandian range of the species *Phellopilus nigrolimiatus*, very little genetic divergence was observed based on population genomic analyses (Sønstebø et al., in prep.). Little genetic differentiation in Eurasia was also observed for the postfire ascomycete *Daldina loculata* (Johannesson et al., 2001), the widespread polypore *F. pinicola* (Högberg et al., 1999), the red-listed *Phlebia centrifuga* (Franzén et al., 2007) and *Fomitopsis rosea* (Högberg & Stenlid, 1999; Kauserud & Schumacher, 2003a). Based on this low level of differentiation, a high dispersal ability is expected.

However, modelling spread of spores in *H. annosum* showed that only 0.1% of the spores spread more than 100 m (Stenlid, 1994). For *Phlebia centrifuga*, spore traps and modelling analyses suggested that spore dispersal is restricted to tens of meters (Nordén & Larsson, 2000; Norros et al., 2012). For more long-distance dispersal, spore deposition was positively correlated to the age of the forest and negatively correlated to forest fragmentation for the five species, *F. pinicola*, *F. rosea*, *P. centrifuga, Trichaptum laricinum* and *Meruliopsis taxicola* (Edman, Gustafsson, Stenlid, & Ericson, 2004; Edman, Gustafsson, Stenlid, Jonsson, et al., 2004). Specifically, for the red-listed species *P. centrifuga* and *F. rosea*, there was a major reduction of spore deposition in more fragmented forests (Edman, Gustafsson, Stenlid, & Ericson, 2004). Nevertheless, even for *T. laricinum* that had the lowest spore deposition, more than 10 spores per m^2 per 24h were found (Edman, Gustafsson, Stenlid, Jonsson, et al.,

2004). There are probably additional factors, as available substrate or competition with other species, that restricts the red-listed *F. rosea* and *P. centrifuga*.

Thus, even with the abundant spore production of these species, there is not much evidence suggesting that ligninolytic fungi often disperse long distances. Spore survival during the dispersal process is affected by variables as UV radiation and temperature (Norros et al., 2015), spore size (Norros et al., 2014), and time of dispersal (Oneto et al., 2020). Thus, a successful dispersal of an individual is dependent on spore dispersal, survival and establishment.

4. Distribution and adaptation

Which wood decay species can be found on a log is dependent on numerous variables, e.g. the local environment, host tree, substrate size, which other species are present in the wood, who have lived in the substrate previously, and the decay stage. Wood decay is a highly specialized process; thus, wood decay species are often adapted to different tree species that have different biochemical composition. Further, fungi are affected by various environmental factors, such as temperature and precipitation (Andrew, Heegaard, et al., 2018). A recent study based on diversity surveys of 180 plots in a mixed forest in Germany, suggested that substrate is more important than the environment for the distribution of wood decay fungi (Krah, Seibold, et al., 2018).

4.1 *Habitat specificity and substrate specialization*

All wood consists of lignocellulose. Lignocelluose is a recalcitrant material consisting of cellulose, hemicellulose, lignin, in addition to pectin, proteins, fatty acids and a set of extractives. However, the substrate experienced by the wood decay fungi can still be highly variable. The proportions of the lignocellulose components vary between gymnosperms and angiosperms, among different species, and even between different parts of an individual tree (Kollmann & Cote, 1968; Sjöström, 1993). When comparing angiosperm and gymnosperm trees, it is generally found that angiosperm trees have more cellulose and less lignin than gymnosperm trees (Table 1). Further, gymnosperm trees have more extractives in the plant cell wall matrix. In addition, there are differences in the amount and type of hemicellulose among the tree species, where angiosperms have more xylans and glucomannanas, and gymnosperms

have more galactoglucomannans (Sjöström, 1993). These are all elements the fungi adapt and respond to in their habitat.

Historically, wood decay fungi have been divided into soft rot, brown rot and white rot based on the morphology and coloring of the decayed wood. Soft rot is mainly caused by ascomycetes, from several different groups, e.g. *Trichoderma*, *Xylaria*, *Aspergillus* (Eurotiales) and *Phialophora* (Chaetothyriales). White and brown rot are caused by basidiomycetes in the subphyla agaricomycetes, and evolved by the expansion of peroxidases that break down lignin through oxidation. Examples of genera with species causing white rot are *Phanerochaete*, *Fomes*, *Trametes*, *Heterobasidion* and *Trichaptum*, and examples of genera with species causing brown rot are *Serpula* and *Fomitopsis*.

Brown rot species have evolved repeatedly and independently from various white rot ancestors (Floudas et al., 2012; Hibbett & Donoghue, 2001). Although independent events, the transition from white rot to brown rot follows some common evolutionary trajectories. First, the processes have involved loss of genes encoding enzymes important for the white rot decay mechanisms, as the peroxidases (Floudas et al., 2012; Riley et al., 2014; for a summary of the relevant enzymes, see also Lundell et al., 2014). The amount of gene loss varies among species and the transition between white rot and brown rot is a more continuous transition than previously thought, with some species having a more intermediate decay mechanism (Riley et al., 2014). Secondly, the rapid wood decay by brown rot species has later been explained by a more efficient redox reaction to deconstruct the lignocellulose complex (Arantes & Goodell, 2014; Koenigs, 1974; Zhang et al. 2016). Consequently, the brown rot fungus can then utilize the carbohydrate polymers of the wood, while leaving the slightly modified lignin as a brown residue (hence the name brown rot). More details about the evolution of wood decay mechanisms are found in the chapter by Floudas in this volume.

Ligninolytic fungal species are all specialized to their niche, but the breath of these niches varies. While some species have a narrow niche, adapted to decaying wood from one species, others can colonize a large variety of tree species. Brown rot species are more commonly specialist of gymnosperms than angiosperms, and the opposite is the case for white rot fungi (Gilbertson, 1980; Hibbett & Donoghue, 2001). In a recent study it was found that white rot fungi more commonly have evolved from being a generalist to angiosperm specialist, while brown rot fungi tend to evolve to become a generalist species (Krah, Bässler, et al., 2018).

There have been several studies on the evolution of substrate specificity in close relatives. For examples, the previously cryptic species in the *Heterobasidion abietinum*, *H.*

parviporum and *H. occidentale* clade cannot infect species of the genus *Pinus*, while the *H. annosum* s.s. and *H. irregulare* clade could infect *Pinus* (Dalman et al., 2010; Garbelotto et al., 1998; Garbelotto & Gonthier, 2013; Johannesson & Stenlid, 2003). Hybrids between these two clades could not decay *Pinus* wood efficiently, thus, substrate specialization (through reinforcement as previously discussed) may maintain species boundaries within *Heterobasidion* (Garbelotto et al., 2007).

Similarly, two evolutionary lineages of *Meruliopsis taxicola*, with different substrate preferences, occur throughout the Nordic countries (Kauserud, Hofton, et al., 2007; Seierstad et al., 2013). One lineage is mainly found on pine in coastal areas, while the other lineage grows mainly on spruce in inland areas. In Norway the separation of the two lineages is maintained, while in Finland they reproduce throughout the distribution. Interestingly, genetic analyses of these lineages only found the pine haplotype growing on spruce in dikaryotic individual (sporocarp) that also possessed the other haplotype (i.e. a hybrid between these two lineages) (Kauserud, Hofton, et al., 2007; Seierstad et al., 2013). Whether lineages isolated from pine have lower performance on spruce, or whether there are reproductive barriers between these two lineages in Norway is unknown and is a topic for further research.

The brown rot decay species *Serpula lacrymans*, is suggested to be adapted to a niche with large substrates, but little nitrogen - as would be expected in the built environment, and in its natural habitat in high mountain areas (Hess et al., 2021). The ability of this species to decay wood in a rapid manner has been well documented (Jennings & Bravery, 1991). It decays certain substrates more rapidly than its sister species *S. himantioides* (Balasundaram et al., 2018; Skrede et al., 2011). Thus, it seems that *S. lacrymans* is adapted to a narrower niche than its more widespread sister species, *S. himantioides* (Balasundaram et al., 2018; Hess et al., 2021). *Serpula* genomes contain relatively many CAZymes compared to other brown rot species (Balasundaram et al., 2018; Eastwood et al., 2011; Floudas et al., 2012; Riley et al., 2014). The number of CAZymes is fewer in *S. lacrymans* than in *S. himantioides*, suggesting that *S. lacrymans* has an increased reliance on the energy efficient non-enzymatic decay system that characterize brown rot decay (Hess et al., 2021). During this adaptation to rapid decay, *S. lacrymans* has become a poor competitor for its substrate, as *S. lacrymans* had significantly poorer competitive ability compared to *S. himantioides* (Balasundaram et al., 2018; Hess et al., 2018).

Competitive interactions among basidiomycete wood decay fungi are known to be important for the decomposition process (Boddy, 2000; Hiscox et al., 2018). Fungi can defend

their substrate in various ways by e.g. altering the pH of the wood, exuding oxidative enzymes or producing volatiles. Primary colonizers are often adapted to rapidly capturing the substrate, at the expense of an effective defense system. Those species entering the community at later decay stages need to outcompete these primary colonizers in order to establish and usually have a more developed competitive repertoire of secondary metabolites (Boddy & Hiscox, 2016; Hiscox & Boddy, 2017). Thus, wood decay species are known to decay the substrate in a successional fashion, where some species are dependent on the wood decay of certain other species in order to decay the wood, while they are hindered by other species. For example, the wood decay species *Phlebiopsis gigantea* is used in the forest industry as a biocontrol agent to stop infections by *H. annosum*, as *the latter* cannot outcompete *P. gigantea* (Garbelotto & Gonthier, 2013). *Phlebiopsis gigantea* does not kill living threes, as *H. annosum* does, thus a much-preferred fungal species for the forest owners. Another example is *Phanerochaete magnolia* that specifically replaces *Datronia mollis* (Ainsworth & Rayner, 1991). Recently it was shown that the size of the mycelium also affects the competitive ability, thus fungi occupying larger substrates have a better defense ability (but slower decomposition rate) than those individuals occupying smaller substrates (Fukasawa et al., 2020). Competitive ability is among the traits that are most positive correlated to decomposition rate and extension rate in a range of basidiomycete wood decay fungi (Lustenhouwer et al., 2020; Maynard et al., 2019). Thus, this indicates that fast growth and defending its substrate are important success factors for wood decay fungi.

4.2 Environmental and climatic effects on fungal distribution

Even if substrate and competition for the substrate are important for the distribution of fungal species, there is no doubt that other environmental variables, including temperature and precipitation are also explaining the occurrences and success of fungi (Andrew, Heegaard, et al., 2018; Gange et al., 2007; Kauserud et al., 2012; Maynard et al., 2019; Wollan et al., 2008). Recently it has been shown that fungal occurrences in both space and time have been altered as a consequence of climate change (based on historical collection and weather data). In high mountain areas many species are now fruiting in higher altitude than previously (Diez et al., 2020). Autumn fruiting species in Europe have now wider seasons in central Europe but shorter season in Northern Europe, while the opposite is the case for spring fruiting species (Andrew, Heegaard, et al., 2018; Gange et al., 2007; Kauserud et al., 2012).

There are several local conditions that affect the fungal diversity on logs, like moisture level. For fungal wood decay to occur, the wood needs at least 30% moisture, where 40-80% is optional (Goodell et al., 2020). The above-mentioned study on decomposition rate and competition ability, found that optimal moisture condition was positively correlated to decomposition rate, but a wide moisture tolerance gradient was negatively related to decomposition rate (Lustenhouwer et al. 2020). A strong negative correlation between optimal moisture and extension rate was also found by Maynard et al. (2019). Thus, adapting to a wide moisture tolerance niche is maybe at the cost of rapid decomposition. At higher moisture level the oxygen levels become scarce and the decay efficiency declines for most species, even if some soft rot ascomycete species can decay wet wood. Thus, logs in humid conditions as those that have fallen into rivers, mires or lakes will often be decomposed at a slower rate, and by a specific fungal community dominated by ascomycetes. Interestingly, a study of the diversity in driftwood in the arctic revealed a high diversity of ascomycetes (Rama et al., 2016), which could probably be explained both by the moisture level of the wood, but also by the marine elements. In general, there are more ascomycetes than basidiomycetes found in marine habitats, even if the fungal diversity in the oceans is still poorly known (Amend et al., 2019).

Fire is another factor that will affect the diversity of wood decay fungi (Edman & Eriksson, 2016). There are several species that are adapted to decaying fire-damaged wood, e.g. *Antrodia sinuosa*, *Daldinia loculata* and *Neurospora crassa*. During a confrontation experiment where *A. sinuosa* competed on wood discs with five other species, it was never outcompeted on burnt wood discs, but lost in about 40% of the cases on the regular discs (Edman & Eriksson, 2016). In a specific confrontation experiment with *F. pinicola*, *A. sinuosa* won 100% of the experiments on burnt wood, but won less than 10% of the cases on regular wood (most cases were a draw). Thus, growth on burnt wood clearly alters the competing ability of these species.

In areas with dead wood, but for some reason few large living trees and absence of canopy (e.g. following avalanches or clear-cutting), there are certain species that are specifically adapted to the rapid change of temperature, and the direct heat from the sun, e.g. *Gloeophyllum sepiarium, Antrodia xantha, Pyconoporus cinnabarinus* and *Dacrymyces stillatus*. This adaptation has made *G. sepiarium* and *D. stillatus* specifically challenging for home owners, as they grow directly on the outer surface of wooden houses (Alfredsen et al., 2005).

549 Saprotrophic fungi are known to be affected by nutrients and pollution, as was shown by
550 the correlation between fungal occurrence data and nitrogen deposition (Andrew, Halvorsen, et
551 al., 2018). Boreal forest is affected by increasing nitrogen deposition in areas affected by
552 anthropogenic activities as agriculture and industry, but also by direct fertilization (Phoenix et
553 al., 2006). However, wood is a nitrogen-poor substrate, and most ligninolytic fungi are adapted
554 to efficient nitrogen usage, e.g. through recycling of nitrogen from old to new mycelia
555 (summarized in Watkinson et al., 2006). How ligninolytic fungi respond to abundant nitrogen
556 is insufficiently known, but there are some indications that increased nitrogen leads to increased
557 diversity of saprotrophs (Morrison et al., 2016) and decomposition of a higher diversity of
558 organic compounds (Gartner et al., 2004). This observation is in contrast to mycorrhizal species,
559 where reduced growth and diversity have repeatedly been observed with increased nitrogen
560 level (Ekblad et al., 2013; Högberg et al., 2003; Högberg et al., 2011; Morrison et al., 2016;
561 Nilsson & Wallander, 2003; van Diepen et al., 2010).

562 To summarize, there are many factors affecting the occurrence of wood decay fungi, such
563 as substrate, temperature, moisture and precipitation, nitrogen deposition, all affecting the
564 success and occurrence of different ligninolytic fungi. Overall, indicating fungi specialize and
565 adapt accordingly to these factors.

566

567 ### *4.3 Local adaptation in ligninolytic fungi*

568 While it has been possible to observe species distribution and link this to the various climatic
569 and environmental variables, the current available genomic tools allow us to understand the
570 genomic basis and the possibilities of local adaptation.

571 Fungal species adapt to their habitat and environment, i.e., some species may fruit later in
572 colder climate, and grow quicker with shorter growth season, others have the ability to grow in
573 nutrient-poor conditions, in the direct sunlight, and so on. There have been a few game-
574 changing studies, where genomic tools have allowed to understand some of the genetic
575 mechanisms that are involved in adaptation. Ellison et al. (2011) found that *N. crassa*, from
576 Louisiana (US) grew more rapidly in colder conditions than the populations collected in warmer
577 climate in the Caribbean. Two genomic regions were more divergent than the average
578 divergence between the genomes of these populations. In these regions, genes related to
579 temperature response and circadian oscillations were present, indicating that temperature

tolerance and possibly a response to daylength were important for adapting to the habitat in a south-north gradient.

In a recent study of *P. nigrolimitatus*, a weak population genetic structure was found in Fennoscandia using RAD sequencing of 327 individuals (Sønstebø et al., in prep.). In this study, they observed associations between numerous genetic loci and variables explaining temperature and precipitation. In addition, an increased linkage disequilibrium among loci correlated to climate was observed, suggesting that epistatic interactions allow large parts of the genome to adapt to climate (Sønstebø et al., in prep.).

Serpula lacrymans, that has adapted to a rapid wood decay compared to its sister species, and has also gone through local adaptation within species. *Serpula lacrymans* in the built environment in Europe, America, Australia and New Zealand is one genetically depauperated population with only a few vegetative incompatibility types and mating type alleles (Kauserud, 2004; Kauserud et al., 2006; Maurice et al., 2014; Skrede et al., 2021). In contrast, high population diversity population is found in Japan. Demographic modelling based on population genomic data showed that these two populations split at least 8000 years before present, indicating two independent invasions into the built environment (Skrede et al., 2021). Both populations seem to have conserved genetic functions related to rapid growth, indicating the importance of this trait in the built environment (Hess et al., 2021, Skrede et al., 2021).

Several other genomic studies of wood decay fungi have shown the importance of enzymes related to the degradation of the lignocellulose of the plant cell wall during the adaptation to the woody substrate in ligninolytic fungi, but mainly on higher taxonomic levels, e.g. in *Fistulina* and *Pycnoporus* (Floudas et al., 2015; Miyauchi et al., 2020). On a population level, however, there are few studies on local adaptation in ligninolytic fungi. In other organisms, it was recently found that larger chromosomal rearrangements and introgressions among species are involved in local adaptation in sunflowers (*Helianthus*) – e.g. a large haplotype block that resulted from introgression from *Helianthus annuus*, was responsible for early flowering in a coastal sunflower population of *Helianthus argophyllus* (Todesco et al., 2020). Large chromosomal rearrangements are also known in fungal plant pathogens during rapid adaptations in the arms race between host and pathogen (e.g. Croll et al., 2013). However, whether this is the case for ligninolytic fungi is still unknown.

4.4 Habitat sensitivity and conservation needs

Deforestation has an effect on water management, desertification, food security and biodiversity loss, and is discussed in detail in the "State of the world's forests" (FAO, 2016). Currently, deforestation is a huge problem in tropical forests, and in the decade of 2000-2010 7 million hectares forests was lost. During the last 5000 years there have been a decline in forests equivalent to 50% of the total forests today (FAO, 2016). However, in temperate regions there is now an increase of forested areas (FAO, 2016). Nevertheless, intense forestry management practices in some regions may leave little dead wood, alter the nutrient availability, fragment suitable habitats, and disturb the soil (Pohjanmies et al., 2017). Thus, for fungi, forest management and other anthropogenic activities affect the amount of suitable substrate, connectivity of the habitat, and size of habitats (Junninen & Komonen, 2011). In Norway about half of all described polypore species are red-listed mainly due to the forest management practices the last centuries (Brandrud et al., 2015).

In danish beech (*Fagus sylvatica*) forests Heilmann-Clausen and Christensen (2005) suggested that managed forests do not have enough large substrates and suitable conditions for many ligninolytic species. Further analyses on the European scale suggested that in order to maintain species diversity and connect fragmented forests, the size of the conserved forests must be larger than today (Abrego et al., 2015; Heilmann-Clausen & Christensen, 2005). This was coherent with the findings from boreal forests, where Nordén et al. (2013) suggested to conserve some large, well-connected areas, rather than many small fragmented regions. The size and decay stage of the substrate are important variables explaining the general species richness and the occurrences of rare species in beech forests (Heilmann-Clausen & Christensen, 2004, 2005).

When the effect of forest fragmentation is investigated for individual species, different trends have been observed. For example, forest fragmentation affected the occurrence of *P. nigrolimitatius* (Stokland & Kauserud, 2004), but not *Cystostereum murrayi* (Sverdrup-Thygeson & Lindenmayer, 2003). These different responses to forest fragmentation could be caused by differences in specialization. Nordén et al. (2013) estimated the degree of specialization in a set of wood decay species and showed that common and widespread species as *F. pinicola* and *T. abietinum* have a broader niche, while several species connected to old-growth forests have narrow niches e.g. *Amylocystis lapponica* and *F. rosea*. Recent studies have also modelled that the more specialized species are more affected by habitat loss, loss of connectivity, and have a higher extinction rate and lower colonization rate (Moor et al., 2020;

Nordén et al., 2013). Thus, the more specialized a species is, the more prone it is for extinction, and the more sensitive to habitat change and forest fragmentation. This is also the case for species that are specialized to co-occur or compete with other species, where recent studies have shown that forest fragmentation has a negative effect on species interactions, thus those that are dependent on other species are more negatively affected by forest fragmentation (Abrego et al., 2017; Rybicki et al., 2020).

Forest fragmentation was suggested to affect population divergence and genetic diversity of *P. centrifuga* (Franzén et al., 2007). It is important to acknowledge that the generation time of wood decay species may vary extensively, which again will affect the observed genetic diversity and divergence. The above mentioned, *P. nigrolimitatus*, may fruit on old logs, while *T. abietinum* fruits on logs that are recently fallen. Thus, there may be a lag from when the species are affected by habitat fragmentation to when a population bottleneck is possible to observe in the genetic material.

In the future, conservation efforts should better consider the needs of the wood decay fungi, and evaluate the habitat size, size and amount of substrate and other needs of these species to retain genetic diversity, and for successful mating to occur. In order help species reestablish, there are ongoing research projects testing the possibility to reintroduce locally extinct species, summarized in Nordén et al. (2020). Already, successful establishment after reintroduction was observed for several species in Finland (e.g. *Amylocystis lapponica*, *A. citrinella* and *F. rosea*) (Abrego et al., 2016) and for *Hericium coralloides* in the UK (Boddy et al., 2011). Such experiments have several challenges, i.e. how will these reintroduced species affect the community that is already there? and how will the low genetic diversity and population size affect the ability for this species to adapt to local environmental factors? As discussed earlier in this chapter, species need to adapt to the current local environment and to climate change, and their chances to adapt are depended on the genetic variability available in the genome. For suggestions on how to handle some of the challenges of reintroduction, see Nordén et al. (2020) on ten principles for conservation translocation.

5. Conclusions and Future perspectives

Ligninolytic fungi are highly adapted to their substrate, but their niches are still highly variable. Some fungi have wide distributions, decay a wide set of woody substrates and have large population sizes. Others are highly specialized to a specific substrate, have small endemic

distributions and have small population sizes. This variety makes ligninolytic fungi interesting for studies on evolutionary and ecological questions. The development of genomic tools, that now allows full genome sequencing of ligninolytic fungi for a low price, opens possibilities to test hypotheses on the mechanisms that allow or restrict, local adaptation and species divergence on non-model organisms. We still do not know how fast species adapt to their local environment, and what the genetic prerequisites are, for a species to be able to adapt to rapid climate changes and habitat fragmentation. As ligninolytic fungi are responsible for a major part of the decomposition of wooden materials, they are important players of the carbon cycle, both releasing carbon to the atmosphere and storing carbon in the soil.

More research is needed to understand the effect of various forest management practices. Currently, it is known that intense forestry practices, such as clear-cutting of large areas, fragment the forests and affect the success of many ligninolytic species. It has been suggested that continuous-cover forestry where the timing of felling, thinning level and regeneration method are carefully monitored to optimized forest diversity, can maintain higher diversity without having to compromise on the economic profit for the forest owners (Eyvindson et al., 2018). However, more research and further political initiatives are needed to establish forest management practices that are optimized for species diversity, low climate impact, profit for the forest owners and the societal need for forest products.

An accurate estimate of the richness and the functional role of these species in their habitat are important as species are becoming extinct before we even discover that they exist. Fungal ligninolytic species have a large variety of ecological roles and are important for the survival of other species in their ecosystem. As the climate change and the land use is altered, we will lose species that are still undescribed, unfortunately, without the possibility to apply any conservation measures. This strongly calls for further research in fungal systematics, fungal diversity, functional genomics, forest ecology and carbon sequestrations, to obtain a more complete understanding of the diversity and the ecological role of ligninolytic fungi.

Acknowledgments

I thank Håvard Kauserud and Sundy Maurice for valuable comments on an earlier version of this chapter. Håvard Kauserud also provided the sketch for Figure 2. I acknowledge the Research Council of Norway project 274337 for funding.

References

Abrego, N., Bässler, C., Christensen, M., & Heilmann-Clausen, J. (2015). Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biological Conservation*, *191*, 469–477.

Abrego, N., Dunson, D., Halme, P., Salcedo, I., & Ovaskainen, O. (2017). Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. *Oikos*, *126*, 269–275.

Abrego, N., Oivanen, P., Viner, I., Nordén, J., Penttilä, R., Dahlberg, A., et al. (2016). Reintroduction of threatened fungal species via inoculation. *Biological Conservation*, *203*, 120–124.

Ainsworth, A. M., & Rayner, A. D. M. (1991). Ontogenetic stages from coenocyte to basidiome and their relation to phenoloxidase activity and colonization processes in *Phanerochaete magnoliae*. *Mycological Research*, *95*, 1414–1422.

Alfredsen, G., Solheim, H., & Jenssen, K. (2005). *Evaluation of decay fungi in Norwegian buildings*. The International Research Group on Wood Protection, IRG/WP 05-10562.

Amend, A., Burgaud, G., Cunliffe, M., Edgcomb, V. P., Ettinger, C. L., Gutiérrez, M. H., et al. (2019). Fungi in the marine environment: Open questions and unsolved problems. *MBio*, *10*, e01189-18.

Anderson, J. B., Bruhn, J. N., Kasimer, D., Wang, H., Rodrigue, N., & Smith, M. L. (2018). Clonal evolution and genome stability in a 2500-year-old fungal individual. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20182233.

Anderson, J. B., & Kohn, L. M. (2007). Dikaryons, Diploids, and Evolution. In *Sex in Fungi*. ASM Press.

Anderson, J. B., Korhonen, K., & Ullrich, R. C. (1980). Relationships between European and North American biological species of *Armillaria mellea*. *Experimental Mycology*, *4*, 78–86.

Anderson, J. B., & Ullrich, R. C. (1979). Biological species of *Armillaria mellea* in North America. *Mycologia*, *71*, 402–414.

Andrew, C., Halvorsen, R., Heegaard, E., Kuyper, T. W., Heilmann-Clausen, J., Krisai-Greilhuber, I., et al. (2018). Continental-scale macrofungal assemblage patterns correlate with climate, soil carbon and nitrogen deposition. *Journal of Biogeography*, *45*, 1942–1953.

Andrew, C., Heegaard, E., Høiland, K., Senn-Irlet, B., Kuyper, T. W., Krisai-Greilhuber, I., et al. (2018). Explaining European fungal fruiting phenology with climate variability. *Ecology*, *99*, 1306–1315.

Arantes, V., & Goodell, B. (2014). *Current understanding of brown-rot fungal biodegradation mechanisms: A review* (Vol. 1158, pp. 3–21). American Chemical Society.

Balasundaram, S. V., Engh, I. B., Skrede, I., & Kauserud, H. (2015). How many DNA markers are needed to reveal cryptic fungal species? *Fungal Biology*, *119*, 940–945.

Balasundaram, S. V., Hess, J., Durling, M. B., Moody, S., Thorbek, L., Progida, C., et al. (2018). The fungus that came in from the cold: Dry rot's pre-adapted ability to invade buildings. *The ISME Journal*, *12*, 791–801.

751 Baldrian, P., Zrůstová, P., Tláskal, V., Davidová, A., Merhautová, V., & Vrška, T. (2016).
752 Fungi associated with decomposing deadwood in a natural beech-dominated forest.
753 *Fungal Ecology*, *23*, 109–122.

754 Baranova, M. A., Logacheva, M. D., Penin, A. A., Seplyarskiy, V. B., Safonova, Y. Y.,
755 Naumenko, S. A., et al. (2015). Extraordinary genetic diversity in a wood decay
756 mushroom. *Molecular Biology and Evolution* 32, 2775–83.

757 Baumgartner, K., Baker, B. R., Korhonen, K., Zhao, J., Hughes, K. W., Bruhn, J., Bowman et
758 al. (2012). Evidence of natural hybridization among homothallic members of the
759 basidiomycete *Armillaria mellea sensu stricto*. *Fungal Biology*, *116*, 677–691.

760 Bjørnaraa, S. J. (2013). *Indoor population structure of the dry rot fungus,* Serpula lacrymans
761 [Master thesis]. University of Oslo.

762 Blaalid, R., Kumar, S., Nilsson, R. H., Abarenkov, K., Kirk, P. M., & Kauserud, H. (2013).
763 ITS1 versus ITS2 as DNA metabarcodes for fungi. *Molecular Ecology Resources*, *13*,
764 218–224.

765 Blackwell, M. (2011). The fungi: 1, 2, 3 ... 5.1 million species? *American Journal of Botany*,
766 *98*, 426–438.

767 Boddy, L. (2000). Interspecific combative interactions between wood-decaying
768 basidiomycetes. *FEMS Microbiology Ecology*, *31*, 185–194.

769 Boddy, L., Crockatt, M. E., & Martyn Ainsworth, A. (2011). Ecology of *Hericium cirrhatum*,
770 *H. coralloides* and *H. erinaceus* in the UK. *Fungal Ecology, 4,* 163-173

771 Boddy, L., & Hiscox, J. (2016). Fungal ecology: Principles and mechanisms of colonization
772 and competition by saprotrophic fungi. *Microbiology Spectrum*, *4*.

773 Brandrud, T. E., Bendiksen, E., Jordal, J. B., Hofton, T. H., Larsson, K. H., & Køiland, K.
774 (2015). *Fungi* (The Norwegian Red List of Species). Artsdatabanken.
775 https://www.artsdatabanken.no/Rodliste/Artsgruppene/Sopper

776 Buller, A. H. R. (1930). The biological significance of conjugate nuclei in *Coprinus lagopus*
777 and other Hymenomycetes. *Nature*, *126*, 686–689.

778 Carlsen, T., Engh, I. B., Decock, C., Rajchenberg, M., & Kauserud, H. (2011). Multiple
779 cryptic species with divergent substrate affinities in the *Serpula himantioides* species
780 complex. *Fungal Biology*, *115*, 54–61.

781 Carvalho, D. B., Smith, M. L., & Anderson, J. B. (1995). Genetic exchange between diploid
782 and haploid mycelia of *Armillaria gallica*. *Mycological Research*, *99*, 641–647.

783 Croll, D., Zala, M., McDonald, B. A. (2013). Breakage-fusion-bridge cycles and large
784 insertions contribute to the rapid evolution of accessory chromosomes in a fungal
785 pathogen. *PLOS Genetics*, *9*, e1003567.

786 Crowe, L. K. (1960). The exchange of genes between nuclei of a dikaryon. *Heredity*, *15*(4),
787 397–405.

788 Dalman, K., Olson, A., & Stenlid, J. (2010). Evolutionary history of the conifer root rot
789 fungus *Heterobasidion annosum sensu lato*. *Molecular Ecology*, *19*(22), 4979–4993.

790 Dettman, J. R., Anderson, J. B., & Kohn, L. M. (2008). Divergent adaptation promotes
791 reproductive isolation among experimental populations of the filamentous fungus
792 *Neurospora*. *BMC Evolutionary Biology*, *8*, 35.

793 Dettman, J. R., Jacobson, D. J., & Taylor, J. W. (2003). A multilocus genealogical approach
794 to phylogenetic species recognition in the model eukaryote *Neurospora*. *Evolution;*
795 *International Journal of Organic Evolution*, *57*, 2703–2720.

796 Dettman, J. R., Jacobson, D. J., Turner, E., Pringle, A., & Taylor, J. W. (2003). Reproductive
797 isolation and phylogenetic divergence in *Neurospora*: Comparing methods of species
798 recognition in a model eukaryote. *Evolution*, *57*, 2721–2741.

799 Diez, J., Kauserud, H., Andrew, C., Heegard, E., Krisai-Greilhuber, I., Senn-Irlet, B., et al.
800 (2020). Altitudinal upwards shifts in fungal fruiting in the Alps. *Proceedings of the*
801 *Royal Society B: Biological Sciences*, *287*, 20192348.

802 Dobzhansky, T. (1937). *Genetics and the origin of species*. Colombia University Press.

803 Dunn, B., & Sherlock, G. (2008). Reconstruction of the genome origins and evolution of the
804 hybrid lager yeast *Saccharomyces pastorianus*. *Genome Research*, *18*, 1610–1623.

805 Eastwood, D. C., Floudas, D., Binder, M., Majcherczyk, A., Schneider, P., Aerts, A., et al.
806 (2011). The plant cell wall-decomposing machinery underlies the functional diversity
807 of forest fungi. *Science*, *333*, 762–765.

808 Eberlein, C., Hénault, M., Fijarczyk, A., Charron, G., Bouvier, M., Kohn, L. M., et al. (2019).
809 Hybridization is a recurrent evolutionary stimulus in wild yeast speciation. *Nature*
810 *Communications*, *10*, 923.

811 Edman, M., & Eriksson, A.-M. (2016). Competitive outcomes between wood-decaying fungi
812 are altered in burnt wood. *FEMS Microbiology Ecology*, *92*, fiw068.

813 Edan, M., Gustafsson, M., Stenlid, J., & Ericson, L. (2004). Abundance and viability of
814 fungal spores along a forestry gradient—Responses to habitat loss and isolation?
815 *Oikos*, *104*, 35–42.

816 Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B. G., & Ericson, L. (2004). Spore
817 deposition of wood-decaying fungi: Importance of landscape composition. *Ecography*,
818 *27*, 103–111.

819 Ekblad, A., Wallander, H., Godbold, D. L., Cruz, C., Johnson, D., Baldrian, P., et al. (2013).
820 The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in
821 forest soils: Role in carbon cycling. *Plant and Soil*, *366*, 1–27.

822 Ellingboe, A. H., & Raper, J. R. (1962). The Buller phenomenon in *Schizophyllum commune*:
823 Nuclear selection in fully compatible dikaryotic-homokaryotic matings. *American*
824 *Journal of Botany*, *49*, 454–459.

825 Ellison, C. E., Hall, C., Kowbel, D., Welch, J., Brem, R. B., Glass, N. L., et al. (2011).
826 Population genomics and local adaptation in wild isolates of a model microbial
827 eukaryote. *Proceedings of the National Academy of Sciences of the United States of*
828 *America*, *108*, 2831–2836.

829 Estensmo, E. L. F., Maurice, S., Morgado, L., Martin-Sanchez, P. M., Skrede, I., & Kauserud,
830 H. (2021). The influence of intraspecific sequence variation during DNA
831 metabarcoding: A case study of eleven fungal species. *Molecular Ecology Resources*,
832 21, *1141-1148*.

833 Eyvindson, K., Repo, A., & Mönkkönen, M. (2018). Mitigating forest biodiversity and
834 ecosystem service losses in the era of bio-based economy. *Forest Policy and*
835 *Economics*, *92*, 119–127.

836 FAO. (2016). *State of the World's Forests*. Forest and agriculture:land-use challenges and
837 opportunities, Rome.

838 Ferguson, B. A., Dreisbach, T. A., Parks, C. G., Filip, G. M., & Schmitt, C. L. (2003).
839 Coarse-scale population structure of pathogenic *Armillaria* species in a mixed-conifer
840 forest in the Blue Mountains of northeast Oregon. *Canadian Journal of Forest*
841 *Research*, *33*, 612–623.

842 Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R. A., Henrissat, B., et al. (2012).
843 The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal
844 genomes. *Science*, *336*(6089), 1715–1719.

845 Floudas, D., Held, B. W., Riley, R., Nagy, L. G., Koehler, G., Ransdell, A. S., et al. (2015).
846 Evolution of novel wood decay mechanisms in Agaricales revealed by the genome
847 sequences of *Fistulina hepatica* and *Cylindrobasidium torrendii*. *Fungal Genetics and*
848 *Biology*, *76*, 78–92.

849 Franzén, I., Vasaitis, R., Penttilä, R., & Stenlid, J. (2007). Population genetics of the wood-
850 decay fungus *Phlebia centrifuga* P. Karst. In fragmented and continuous habitats.
851 *Molecular Ecology*, *16*(16), 3326–3333.

852 Fukasawa, Y., Gilmartin, E. C., Savoury, M., & Boddy, L. (2020). Inoculum volume effects
853 on competitive outcome and wood decay rate of brown- and white-rot basidiomycetes.
854 *Fungal Ecology*, *45*, 100938.

855 Gange, A. C., Gange, E. G., Sparks, T. H., & Boddy, L. (2007). Rapid and recent changes in
856 fungal fruiting patterns. *Science*, *316*, 71.

857 Garbelotto, M., & Gonthier, P. (2013). Biology, epidemiology, and control of *Heterobasidion*
858 species worldwide. *Annual Review of Phytopathology*, *51*, 39–59.

859 Garbelotto, M., Gonthier, P., & Nicolotti, G. (2007). Ecological constraints limit the fitness of
860 fungal hybrids in the *Heterobasidion annosum* species complex. *Applied and*
861 *Environmental Microbiology*, *73*, 6106–6111.

862 Garbelotto, M., Otrosina, W. J., Cobb, F. W., & Bruns, T. D. (1998). The European S and F
863 intersterility groups of *Heterobasidion annosum* may represent sympatric
864 protospecies. *Canadian Journal of Botany*, *76*, 397–409.

865 Gartner, T., Turner, K., & Treseder, K. (2004). Nitrogen additions increase the diversity of
866 carbon compounds degraded by fungi in boreal forests. *AGU Fall Meeting Abstracts*.

867 Gates, G. M., Mohammed, C., Wardlaw, T., Ratkowsky, D. A., & Davidson, N. J. (2011).
868 The ecology and diversity of wood-inhabiting macrofungi in a native *Eucalyptus*
869 *obliqua* forest of southern Tasmania, Australia. *Fungal Ecology*, *4*, 56–67.

870 Gilbertson, R. L. (1980). Wood-rotting fungi of North America. *Mycologia*, *72*, 1–49.

871 Giraud, T., Refrégier, G., Le Gac, M., de Vienne, D. M., & Hood, M. E. (2008). Speciation in
872 fungi. *Fungal Genetics and Biology*, *45*, 791–802.

873 Gladieux, P., Ropars, J., Badouin, H., Branca, A., Aguileta, G., de Vienne, D. M., et al.
874 (2014). Fungal evolutionary genomics provides insight into the mechanisms of
875 adaptive divergence in eukaryotes. *Molecular Ecology*, *23*, 753–773.

876 Goodell, B., Winandy, J. E., & Morrell, J. J. (2020). Fungal degradation of wood: Emerging
877 data, new insights and changing perceptions. *Coatings*, *10*, 1210.

878 Haight, J.-E., Laursen, G. A., Glaeser, J. A., & Taylor, D. L. (2016). Phylogeny of *Fomitopsis*
879 *pinicola*: A species complex. *Mycologia*, *108*, 925–938.

880 Hawksworth, D. L. (1991). The fungal dimension of biodiversity: Magnitude, significance,
881 and conservation. *Mycological Research*, *95*, 641–655.

882 Hawksworth, D. L., & Lucking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million
883 species. *Microbiology Spectrum*, *5*.

884 Heilmann-Clausen, J., & Christensen, M. (2004). Does size matter?: On the importance of
885 various dead wood fractions for fungal diversity in Danish beech forests. *Forest*
886 *Ecology and Management*, *201*, 105–117.

887 Heilmann-Clausen, J., & Christensen, M. (2005). Wood-inhabiting macrofungi in Danish
888 beech-forests – conflicting diversity patterns and their implications in a conservation
889 perspective. *Biological Conservation*, *122*, 633–642.

890 Hess, J., Balasundaram, S. V., Bakkemo, R. I., Drula, E., Henrissat, B., Högberg, N.,
891 Eastwood, D., & Skrede, I. (2021). Niche differentiation drives evolution of the wood
892 decay machinery in the invasive fungus *Serpula lacrymans*. *The ISME Journal*, *15*,
893 592–604.

894 Hess, J., Skrede, I., Chaib de Mares, M., Hainaut, M., & Henrissat, B. (2018). Rapid
895 divergence of genome architectures following the origin of an ectomycorrhizal
896 symbiosis in the genus *Amanita*. *Molecular Biology and Evolution*, *35*, 2786–2804.

897 Hibbett, D. S., & Donoghue, M. J. (2001). Analysis of character correlations among wood
898 decay mechanisms, mating systems, and substrate ranges in Homobasidiomycetes.
899 *Systematic Biology*, *50*, 215–242.

900 Hiscox, J., & Boddy, L. (2017). Armed and dangerous – chemical warfare in wood decay
901 communities. *Fungal Biology Reviews*, *31*, 169-184.

902 Hiscox, J., O'Leary, J., & Boddy, L. (2018). Fungus wars: Basidiomycete battles in wood
903 decay. *Studies in Mycology*, *89*, 117–124.

904 Högberg, M. N., Bååth, E., Nordgren, A., Arnebrant, K., & Högberg, P. (2003). Contrasting
905 effects of nitrogen availability on plant carbon supply to mycorrhizal fungi and
906 saprotrophs – a hypothesis based on field observations in boreal forest. *New*
907 *Phytologist*, *160*, 225–238.

908 Högberg, N., Holdenrieder, O., & Stenlid, J. (1999). Population structure of the wood decay
909 fungus *Fomitopsis pinicola*. *Heredity*, *83*, 354–360.

910 Högberg, N., & Stenlid, J. (1999). Population genetics of *Fomitopsis rosea* – a wood-decay
911 fungus of the old-growth European taiga. *Molecular Ecology*, *8*, 703–710.

912 Högberg, P., Johannisson, C., Yarwood, S., Callesen, I., Näsholm, T., Myrold, D. D., et al.
913 (2011). Recovery of ectomycorrhiza after "nitrogen saturation" of a conifer forest. *The*
914 *New Phytologist*, *189*, 515–525.

915 Hopkins, R. (2013). Reinforcement in plants. *The New Phytologist*, *197*, 1095–1103.

916 Hottola, J., Ovaskainen, O., & Hanski, I. (2009). A unified measure of the number, volume
917 and diversity of dead trees and the response of fungal communities. *Journal of*
918 *Ecology*, *97*, 1320–1328.

James, T. Y., Porter, D., Hamrick, J. L., & Vilgalys, R. (1999). Evidence for limited intercontinental gene flow in the cosmopolitan mushroom, *Schizophyllum commune*. *Evolution*, *53*, 1665–1677.

James, T. Y., Stajich, J. E., Hittinger, C. T., & Rokas, A. (2020). Toward a fully resolved fungal tree of life. *Annual Review of Microbiology*, *74*, 291–313.

James, T. Y., Stenlid, J., Olson, A., & Johannesson, H. (2008). Evolutionary significance of imbalanced nuclear ratios within heterokaryons of the basidiomycete fungus *Heterobasidion parviporum*. *Evolution*, *62*, 2279–2296.

James, T. Y., & Vilgalys, R. (2001). Abundance and diversity of *Schizophyllum commune* spore clouds in the Caribbean detected by selective sampling. *Molecular Ecology*, *10*(2), 471–479.

Jennings, D. H., & Bravery, A. F. (1991). *Serpula lacrymans: Fundamental Biology and Control Strategies*. Wiley-Blackwell.

Jensen, A. L., Kauserud, H., & Maurice, S. (2020). High phenotypic variability in the wood decay fungus *Phellopilus nigrolimitatus*. *Fungal Ecology*, *in press*.

Johannesson, H., Læssøe, T., & Stenlid, J. (2000). Molecular and morphological investigation of *Daldinia* in northern Europe. *Mycological Research*, *104*, 275–280.

Johannesson, H., & Stenlid, J. (2003). Molecular markers reveal genetic isolation and phylogeography of the S and F intersterility groups of the wood-decay fungus *Heterobasidion annosum*. *Molecular Phylogenetics and Evolution*, *29*, 94–101.

Johannesson, H., Vasiliauskas, R., Dahlberg, A., Penttilä, R., & Stenlid, J. (2001). Genetic differentiation in Eurasian populations of the postfire ascomycete *Daldinia loculata*. *Molecular Ecology*, *10*, 1665–1677.

Junninen, K., & Komonen, A. (2011). Conservation ecology of boreal polypores: A review. *Biological Conservation*, *144*, 11–20.

Kauserud, H. (2004). Widespread vegetative compatibility groups in the dry-rot fungus *Serpula lacrymans*. *Mycologia*, *96*, 232–239.

Kauserud, H., Heegaard, E., Büntgen, U., Halvorsen, R., Egli, S., Senn-Irlet, B., et al. (2012). Warming-induced shift in European mushroom fruiting phenology. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 14488–14493.

Kauserud, H., Hofton, T. H., & Saetre, G.-P. (2007). Pronounced ecological separation between two closely related lineages of the polyporous fungus *Gloeoporus taxicola*. *Mycological Research*, *111*, 778–786.

Kauserud, H., Saetre, G.-P., Schmidt, O., Decock, C., & Schumacher, T. (2006). Genetics of self/nonself recognition in *Serpula lacrymans*. *Fungal Genetics and Biology*, *43*, 503–510.

Kauserud, H., & Schumacher, T. (2002). Population structure of the endangered wood decay fungus *Phellinus nigrolimitatus* (Basidiomycota). *Canadian Journal of Botany*, *80*, 597–606.

Kauserud, H., & Schumacher, T. (2003a). Genetic structure of Fennoscandian populations of the threatened wood-decay fungus *Fomitopsis rosea* (Basidiomycota). *Mycological Research*, *107*, 155–163.

961 Kauserud, H., & Schumacher, T. (2003b). Regional and local population structure of the
962 pioneer wood-decay fungus *Trichaptum abietinum*. *Mycologia*, *95*, 416–425.

963 Kauserud, H., & Schumacher, T. (2003c). Ribosomal DNA variation, recombination and
964 inheritance in the basidiomycete *Trichaptum abietinum*: Implications for reticulate
965 evolution. *Heredity*, *91*, 163–172.

966 Kauserud, H., Shalchian-Tabrizi, K., & Decock, C. (2007). Multilocus sequencing reveals
967 multiple geographically structured lineages of *Coniophora arida* and *C. olivacea*
968 (Boletales) in North America. *Mycologia*, *99*, 705–713.

969 Kauserud, H., Svegarden, I. B., Decock, C., & Hallenberg, N. (2007). Hybridization among
970 cryptic species of the cellar fungus *Coniophora puteana* (Basidiomycota). *Molecular*
971 *Ecology*, *16*, 389–399.

972 Kauserud, H., Svegarden, I. B., Saetre, G.-P., Knudsen, H., Stensrud, O., Schmidt, et al.
973 (2007). Asian origin and rapid global spread of the destructive dry rot fungus *Serpula*
974 *lacrymans*. *Molecular Ecology*, *16*, 3350–3360.

975 Koenigs, J. W. (1974). Hydrogen peroxide and iron: A proposed system for decomposition of
976 wood by brown-rot Basidiomycetes. *Wood and Fiber Science*, *6*, 66–80.

977 Kollmann, F. F. P., & Cote, W. A. J. (1968). *Principles of Wood Science and Technology: I*
978 *Solid Wood*. Springer-Verlag.

979 Krah, F.-S., Bässler, C., Heibl, C., Soghigian, J., Schaefer, H., & Hibbett, D. S. (2018).
980 Evolutionary dynamics of host specialization in wood-decay fungi. *BMC Evolutionary*
981 *Biology*, *18*, 119.

982 Krah, F.-S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., & Bässler, C. (2018).
983 Independent effects of host and environment on the diversity of wood-inhabiting
984 fungi. *Journal of Ecology*, *106*, 1428–1442.

985 Langdon, Q. K., Peris, D., Baker, E. P., Opulente, D. A., Nguyen, H.-V., Bond, U., et al.
986 (2019). Fermentation innovation through complex hybridization of wild and
987 domesticated yeasts. *Nature Ecology & Evolution*, *3*, 1576–1586.

988 Libkind, D., Hittinger, C. T., Valerio, E., Goncalves, C., Dover, J., Johnston, M., et al. (2011).
989 Microbe domestication and the identification of the wild genetic stock of lager-
990 brewing yeast. *Proceedings of the National Academy of Sciences of the United States*
991 *of America*, *108*, 14539–14544.

992 Liti, G., Barton, D. B. H., & Louis, E. J. (2006). Sequence diversity, reproductive isolation
993 and species concepts in *Saccharomyces*. *Genetics*, *174*, 839–850.

994 Lundell, T. K., Mäkelä, M. R., de Vries, R. P., & Hildén, K. S. (2014). Chapter Eleven—
995 Genomics, Lifestyles and Future Prospects of Wood-Decay and Litter-Decomposing
996 Basidiomycota. In F. M. Martin (Ed.), *Advances in Botanical Research* (Vol. 70, pp.
997 329–370). Academic Press.

998 Lustenhouwer, N., Maynard, D. S., Bradford, M. A., Lindner, D. L., Oberle, B., Zanne, A. E.,
999 et al. (2020). A trait-based understanding of wood decomposition by fungi.
1000 *Proceedings of the National Academy of Sciences*, *117*, 11551–11558.

1001 Macrae, R. (1967). Pairing incompatibility and other distinctions among *Hirschioporus*
1002 (*Polyporus*) *abietinus*, *H. fusco-violaceus*, and *H. laricinus*. *Canadian Journal of*
1003 *Botany*, *45*, 1371–1398.

Magasi, L. M. (1976). Incompatibility factors in *Polyporus abietinus*, their numbers and distribution. *Memoirs of the New York Botanical Garden*, *28*, 163–173.

Maurice, S., Skrede, I., LeFloch, G., Barbier, G., & Kauserud, H. (2014). Population structure of *Serpula lacrymans* in Europe with an outlook to the French population. *Mycologia*, *106*, 889–895.

Maurice, S., Arnault, G., Nordén, J., Botnen, S. S., Miettinen, O., Kauserud, H. (2021). Fungal sporocarps house diverse and host-specific communities of fungicolous fungi. *The ISME Journal*, *15*, 1445-1457.

Maynard, D. S., Bradford, M. A., Covey, K. R., Lindner, D., Glaeser, J., Talbert, D. A., et al. (2019). Consistent trade-offs in fungal trait expression across broad spatial scales. *Nature Microbiology*, *4*, 846–853.

Miyauchi, S., Hage, H., Drula, E., Lesage-Meessen, L., Berrin, J.-G., Navarro, D., et al. (2020). Conserved white-rot enzymatic mechanism for wood decay in the Basidiomycota genus *Pycnoporus*. *DNA Research*, *27*, dsaa011.

Mohanta, T. K., & Bae, H. (2015). The diversity of fungal genome. *Biological Procedures Online*, *17*, 8.

Moor, H., Nordén, J., Penttilä, R., Siitonen, J., & Snäll, T. (2020). Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *Journal of Ecology*, *109*, 491-503.

Morrison, E. W., Frey, S. D., Sadowsky, J. J., van Diepen, L. T. A., Thomas, W. K., & Pringle, A. (2016). Chronic nitrogen additions fundamentally restructure the soil fungal community in a temperate forest. *Fungal Ecology*, *23*, 48–57.

Mounce, I., & Macrae, R. (1938). Interfertility phenomena in *Fomes pinicola*. *Canadian Journal of Research*, *16*, 354–376.

Niemelä, T., & Ryvarden, L. (1983). *Antrodiella citrinella*: A new polypore species. *Karstenia*, *23*, 26–30.

Nieuwenhuis, B. P. S., Debets, A. J. M., & Aanen, D. K. (2011). Sexual selection in mushroom-forming basidiomycetes. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 152–157.

Nieuwenhuis, B. P. S., & James, T. Y. (2016). The frequency of sex in fungi. *Philosophical Transactions of the Royal Society B*, *371*.

Nilsson, L. O., & Wallander, H. (2003). Production of external mycelium by ectomycorrhizal fungi in a norway spruce forest was reduced in response to nitrogen fertilization. *New Phytologist*, *158*, 409–416.

Nilsson, R. H., Kristiansson, E., Ryberg, M., Hallenberg, N., & Larsson, K.-H. (2008). Intraspecific ITS variability in the kingdom Fungi as expressed in the international sequence databases and its implications for molecular species identification. *Evolutionary Bioinformatics Online*, *4*, 193–201.

Niskanen, T., & Douglas. (2018). New discoveries: Species of fungi described in 2017. In *State of the World's Fungi*.

Nogami, T., Kamemoto, Y., Ohga, S., & Kitamoto, Y. (2002). The buller phenomenon in a bipolar basidiomycetous mushroom, *Pholiota nameko*. *Micología Aplicada International*, *14*, 11–18.

1047 Nordén, B., & Larsson, K.-H. (2000). Basidiospore dispersal in the old-growth fungus
1048 *Phlebia centrifuga* (Basidiomycetes). *Nordic Journal of Botany*, *20*, 215–219.

1049 Nordén, J., Abrego, N., Boddy, L., Bässler, C., Dahlberg, A., Halme, P., et al. (2020). Ten
1050 principles for conservation translocations of threatened wood-inhabiting fungi. *Fungal*
1051 *Ecology*, *44*, 100919.

1052 Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., & Ovaskainen, O. (2013). Specialist species
1053 of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal
1054 forests. *Journal of Ecology*, *101*, 701–712.

1055 Norros, V., Karhu, E., Nordén, J., Vähätalo, A. V., & Ovaskainen, O. (2015). Spore
1056 sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecology*
1057 *and Evolution*, *5*, 3312–3326.

1058 Norros, V., Penttilä, R., Suominen, M., & Ovaskainen, O. (2012). Dispersal may limit the
1059 occurrence of specialist wood decay fungi already at small spatial scales. *Oikos*, *121*,
1060 961–974.

1061 Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T., & Ovaskainen, O. (2014). Do
1062 small spores disperse further than large spores? *Ecology*, *95*, 1612–1621.

1063 Olson, A., & Stenlid, J. (2001). Plant pathogens: Mitochondrial control of fungal hybrid
1064 virulence. *Nature*, *411*, 438–438.

1065 Oneto, D. L., Golan, J., Mazzino, A., Pringle, A., & Seminara, A. (2020). Timing of fungal
1066 spore release dictates survival during atmospheric transport. *Proceedings of the*
1067 *National Academy of Sciences*, *117*, 5134–5143.

1068 Ortiz-Barrientos, D., Counterman, B. A., & Noor, M. A. F. (2004). The genetics of speciation
1069 by reinforcement. *PLoS Biology*, *2*(12), e416.

1070 Ottosson, E., Kubartová, A., Edman, M., Jönsson, M., Lindhe, A., Stenlid, J., et al. (2015).
1071 Diverse ecological roles within fungal communities in decomposing logs of *Picea*
1072 *abies*. *FEMS Microbiology Ecology*, *91*, fiv012.

1073 Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., & Nordén,
1074 J. (2013). Combining high-throughput sequencing with fruit body surveys reveals
1075 contrasting life-history strategies in fungi. *The ISME Journal*, *7*, 1696–1709.

1076 Paoletti, M. (2016). Vegetative incompatibility in fungi: From recognition to cell death,
1077 whatever does the trick. *Fungal Biology Reviews*, *30*, 152–162.

1078 Peris, D., Langdon, Q. K., Moriarty, R. V., Sylvester, K., Bontrager, M., Charron, G., et al.
1079 (2016). Complex ancestries of lager-brewing hybrids were shaped by standing
1080 variation in the wild yeast *Saccharomyces eubayanus*. *PLOS Genetics*, *12*, e1006155.

1081 Phoenix, G. K., Hicks, W. K., Cinderby, S., Kuylenstierna, J. C. I., Stock, W. D., Dentener, F.
1082 J., et al. (2006). Atmospheric nitrogen deposition in world biodiversity hotspots: The
1083 need for a greater global perspective in assessing N deposition impacts. *Global*
1084 *Change Biology*, *12*, 470–476.

1085 Plissonneau, C., Sturchler, A., & Croll, D. (2016). The evolution of orphan regions in
1086 genomes of a fungal pathogen of wheat. *MBio*, *7*, e01231-16.

1087 Pohjanmies, T., Triviño, M., Le Tortorec, E., Mazziotta, A., Snäll, T., & Mönkkönen, M.
1088 (2017). Impacts of forestry on boreal forests: An ecosystem services perspective.
1089 *Ambio*, *46*, 743–755.

1090 Raffaele, S., & Kamoun, S. (2012). Genome evolution in filamentous plant pathogens: Why
1091 bigger can be better. *Nature Reviews. Microbiology*, *10*, 417–430.

1092 Rajchenberg, M. (2011). Nuclear behavior of the mycelium and the phylogeny of Polypores
1093 (Basidiomycota). *Mycologia*, *103*, 677–702.

1094 Rama, T., Davey, M. L., Nordén, J., Halvorsen, R., Blaalid, R., Mathiassen, G. H., Alsos, I.
1095 G., & Kauserud, H. (2016). Fungi sailing the arctic ocean: Speciose communities in
1096 North Atlantic driftwood as revealed by high-throughput amplicon sequencing.
1097 *Microbial Ecology*, *72*(2), 295–304.

1098 Riley, R., Salamov, A. A., Brown, D. W., Nagy, L. G., Floudas, D., Held, B. W., et al. (2014).
1099 Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-
1100 rot/brown-rot paradigm for wood decay fungi. *Proceedings of the National Academy*
1101 *of Sciences of the United States of America*, *111*(27), 9923–9928.

1102 Rowell, R. M. (2012). *Handbook of wood chemistry and wood composites* (2nd ed.). CRC
1103 Press, Taylor and Francis Group, Boca Raton, FL, USA.

1104 Rybicki, J., Abrego, N., & Ovaskainen, O. (2020). Habitat fragmentation and species
1105 diversity in competitive communities. *Ecology Letters*, *23*(3), 506–517.

1106 Ryvarden, L., & Gilbertson, R. L. (1994). *European polypores: Part 2: Meripilus-Tyromyces*.
1107 Fungiflora A/S. https://www.cabdirect.org/cabdirect/abstract/19951000185

1108 Sætre, G.-P., Moum, T., Bures, S., Kral, M., Adamjan, M., & Moreno, J. (1997). A sexually
1109 selected character displacement in flycatchers reinforces premating isolation. *Nature*,
1110 *387*, 589–592.

1111 Saine, S., Ovaskainen, O., Somervuo, P., & Abrego, N. (2020). Data collected by fruit body–
1112 and DNA-based survey methods yield consistent species-to-species association
1113 networks in wood-inhabiting fungal communities. *Oikos*, *129*, 1833–1843.

1114 Sato, H., Ohta, R., & Murakami, N. (2020). Molecular prospecting for cryptic species of the
1115 *Hypholoma fasciculare* complex: Toward the effective and practical delimitation of
1116 cryptic macrofungal species. *Scientific Reports*, *10*, 13224.

1117 Seierstad, K. S., Carlsen, T., Saetre, G.-P., Miettinen, O., Hofton, T. H., & Kauserud, H.
1118 (2013). A phylogeographic survey of a circumboreal polypore indicates introgression
1119 among ecologically differentiated cryptic lineages. *Fungal Ecology*, *6*, 119–128.

1120 Seierstad, K. S., Fossdal, R., Larsson, K.-H., Miettinen, O., Carlsen, T., Skrede, I., &
1121 Kauserud, H. (2021). Contrasting genetic structuring in the closely related
1122 basidiomycetes *Trichaptum abietinum* and *T. fuscoviolaceum* (Hymenochaetales).
1123 *Fungal Biology, 125, 269-275*.

1124 Servedio, M. R., & Noor, M. (2003). The role of reinforcement in speciation: Theory and
1125 data. *Annual Review of Ecology, Evolution and Systematics*, *34*, 339–364.

1126 Sjöström, E. (1993). *Wood chemistry: Fundamentals and applications*. Academic Press.

1127 Skrede, I., Carlsen, T., Stensrud, O., & Kauserud, H. (2012). Genome wide AFLP markers
1128 support cryptic species in *Coniophora* (Boletales). *Fungal Biology*, *116*, 778–784.

1129 Skrede, I., Engh, I. B., Binder, M., Carlsen, T., Kauserud, H., & Bendiksby, M. (2011).
1130 Evolutionary history of the Serpulaceae (Basidiomycota): molecular phylogeny,
1131 historical biogeography and evidence for a single transition of nutritional mode. *BMC*
1132 *Evolutionary Biology, 11*, e230.

Skrede, I., Murat, C., Hess, J., Maurice, S., Sønstebø, J. H., Kohler, A., et al. (2021). Contrasting demographic histories revealed in two invasive populations of the dry rot fungus *Serpula lacrymans*. *Molecular Ecology, in press*.

Smith, M. L., Bruhn, J. N., & Anderson, J. B. (1992). The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature*, *356*, 428–431.

Snider, P. J., & Raper, J. R. (1958). Nuclear migration in the basidiomycete *Schizophyllum commune*. *American Journal of Botany*, *45*, 538–546.

Sønstebø, J. H., Trucchi, E., Nordén, J., Skrede, I. Miettinen, O., Haridas, S., et al.. Landscape genomics of a forest fungus reveals high gene flow and signatures of climate adaptation. *Manuscript in prep*.

Stenlid, J. (1994). *Regional differentiation in* Heterobasidion annosum. 8. International Conference on Root and Butt Rots, Uppsala (Sweden), 9-16 Aug 1993.

Stenlid, J., Penttilä, R., & Dahlberg, A. (2008). Chapter 13 Wood-decay basidiomycetes in boreal forests: Distribution and community development. In L. Boddy, J. C. Frankland, & P. van West (Eds.), *British Mycological Society Symposia Series* (Vol. 28, pp. 239–262). Academic Press.

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, *133*(2), 240–256.

Stokland, J., & Kauserud, H. (2004). *Phellinus nigrolimitatus*—A wood-decomposing fungus highly influenced by forestry. *Forest Ecology and Management*, *187*(2–3), 333–343.

Stokland, J., & Meyke, E. (2008). The saproxylic database: An emerging overview of the biological diversity in dead wood. *Revue d'Ecologie (La Terre et La Vie)*, *63*, 37–48.

Stokland, J., & Siitonen, J. (2012). Species diversity of saproxylic organisms. In B. G. Jonsson, J. Stokland, & J. Siitonen (Eds.), *Biodiversity in Dead Wood* (pp. 248–274). Cambridge University Press.

Stukenbrock, E. H. (2013). Evolution, selection and isolation: A genomic view of speciation in fungal plant pathogens. *The New Phytologist*, *199*, 895–907.

Stukenbrock, E. H., Christiansen, F. B., Hansen, T. T., Dutheil, J. Y., & Schierup, M. H. (2012). Fusion of two divergent fungal individuals led to the recent emergence of a unique widespread pathogen species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 10954–10959.

Sverdrup-Thygeson, A., & Lindenmayer, D. B. (2003). Ecological continuity and assumed indicator fungi in boreal forest: The importance of the landscape matrix. *Forest Ecology and Management*, *174*, 353–363.

Taylor, D. L., Hollingsworth, T. N., McFarland, J. W., Lennon, N. J., Nusbaum, C., & Ruess, R. W. (2014). A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. *Ecological Monographs*, *84*, 3–20.

Taylor, J. W., Hann-Soden, C., Branco, S., Sylvain, I., & Ellison, C. E. (2015). Clonal reproduction in fungi. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 8901–8908.

Taylor, J. W., Jacobson, D. J., Kroken, S., Kasuga, T., Geiser, D. M., Hibbett, D. S., & Fisher, M. C. (2000). Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology*, *31*, 21–32.

Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N. S., Wijesundera, R., et al. (2014). Global diversity and geography of soil fungi. *Science*, *346*, 1256688–1256689.

Tedersoo, L., Bahram, M., Toots, M., Diedhiou, A., Henkel, T., Kjøller, R., et al. (2012). Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology*, *21*, 4160–4170.

Todesco, M., Owens, G. L., Bercovich, N., Légaré, J.-S., Soudi, S., Burge, D. O., et al. (2020). Massive haplotypes underlie ecotypic differentiation in sunflowers. *Nature, 584*, 602–607.

Turner, E., Jacobson, D. J., & Taylor, J. W. (2011). Genetic architecture of a reinforced, postmating, reproductive isolation barrier between *Neurospora species* indicates evolution via natural selection. *PLoS Genetics*, *7*, e1002204-13.

Ullrich, R. C., & Raper, J. R. (1975). Primary homothallism-relation to heterothallism in the regulation of sexual morphogenesis in *Sistotrema*. *Genetics*, *80*, 311–321.

van Diepen, L. T. A., Lilleskov, E. A., Pregitzer, K. S., & Miller, R. M. (2010). Simulated nitrogen deposition causes a decline of intra- and extraradical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests. *Ecosystems*, *13*, 683–695.

Watkinson, S. C., Bebber, D., Darrah, P., Fricker, M., Tlalka, M., & Boddy, L. (2006). *7 The role of wood decay fungi in the carbon and nitrogen dynamics of the forest floor* (G. M. Gadd, Ed.; pp. 1–31).

Wheeler, Q. D., & Meier, R. (Eds.). (2000). *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press.

Wollan, A. K., Bakkestuen, V., Kauserud, H., Gulden, G., & Halvorsen, R. (2008). Modelling and predicting fungal distribution patterns using herbarium data. *Journal of Biogeography*, *35*, 2298–2310.

Zhang, J., Presley, G. N., Hammel, K. E., Ryu, J.-S., Menke J. R., Figueroa, M., et al. (2016). Localizing gene regulation reveals a staggered wood decay mechanism for the brown rot fungus *Postia placenta*. *Proceedings of the National Academy of Sciences, 113*, 10968-10973.

Tables and figure legends

Table 1. Chemical composition of a selection of Angiosperm (above the dotted line) and Gymnosperm (below the dotted line) North American tree species. Numbers are derived from chapter 2 in Kollmann and Côté (1968) and chapter 3 in Rowell (2012), from both oven dried wood, and soluble components.

Wood species	Cellulose %	Hemicellulose %	Lignin %	Extractives %	Ash %
Acer rubrum	45-47	29-30	21-24	5.3	0.3-0.4
Betula papyrifera	42-45	38	18-19		0.3
Fagus grandifolia	45-49	29-32	22	3.4	0.4
Populus tremuloides	48-49	27-30	19-24		0.4
Ulmus americana	50-51	23	22-24	1.9	0.8
Abies balsamea	42	25-27	29	2	0.4
Picea glauca	41-43	28-31	27-29	1	0.3
Pinus strobes	41-45	26-27	27-29	3	0.2
Thuja occidentalis	41-44	23-26	30-31	2	0.5
Tsuga canadensis	41	23	33	3	0.5

[Figure 1, should be one full page]

Figure 1. Various ligninolytic fungi. a) *Ascocoryne sarcoides* sexual stage (teleomorph), Photo: Klaus Høiland, b) *Ascocoryne sarcoides* asexual stage (anamorph), Photo: Klaus Høiland, c) *Xeromphalina campanella*, Photo: Inger Skrede, d) *Bisporella citrina*, Photo: Klaus Høiland, e) *Xylaria hypoxylon* with white asexual conida, Photo: Klaus Høiland, f) *Ganoderma applanatum*, Photo: Inger Skrede, g) *Fomitopsis pinicola*, Photo: Inger Skrede, h) *Crucibulum leave*, Photo: Inger Skrede, i) *Daedalea quercina*, Photo: Inger Skrede, j) *Serpula lacrymans*, Photo: Inger Skrede.

[Figure 2, is prepared as a one-column figure]

Figure 2. A common lifecycle of an Agaricomycete wood decay fungus, exemplified with *Trichaptum abietinum*.

[Figure 3, is prepared as a one-column figure]

Figure 3: Schematic drawing of the number of individuals of *Trichaptum abietinum* on a log, inspired by Kauserud & Schumacher (2003b). Many individuals are often present on the same log. Photo: Inger Skrede.


a)


b)


c)


d)


e)

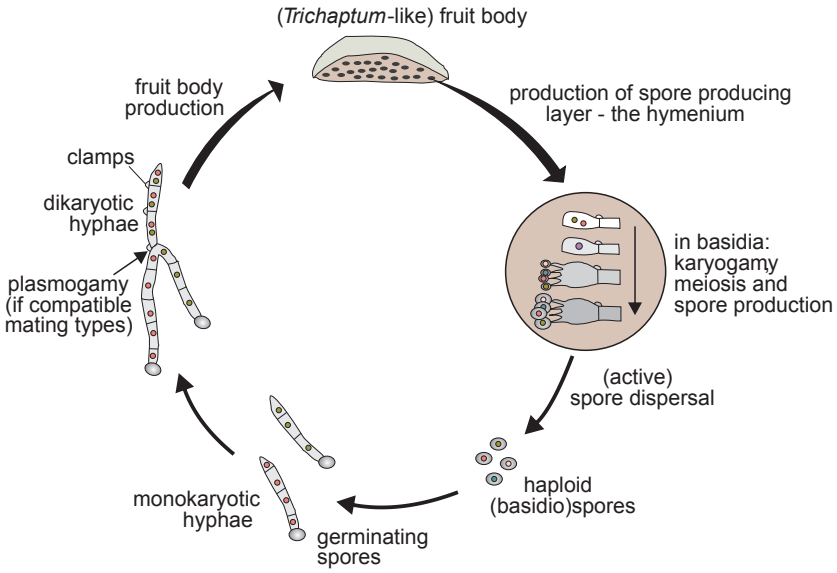

f)

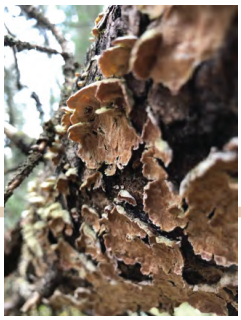

g)


h)


i)


j)


(*Trichaptum*-like) fruit body
production of spore producing layer - the hymenium
in basidia: karyogamy meiosis and spore production
(active) spore dispersal
haploid (basidio)spores
germinating spores
monokaryotic hyphae
plasmogamy (if compatible mating types)
dikaryotic hyphae
clamps
fruit body production



In *Trichaptum abietinum* there are often many individuals on each log