Published in final edited form as:

Microbiol Spectr. 2017 July ; 5(4): . doi:10.1128/microbiolspec.FUNK-0055-2016.

Fungal genomes and insights into the evolution of the kingdom

Jason E Stajich¹

¹Department of Plant Pathology & Microbiology and Institute of Integrative Genome Biology, University of California, Riverside, CA 92521 USA

Summary

The kingdom Fungi comprises species that inhabit nearly all ecosystems. Fungi exist as both free-living and symbiotic unicellular and multicellular organisms with diverse morphologies [1]. The genomes of fungi encode genes that enable them to thrive in diverse environments, invade plant and animal cells, and participate in nutrient cycling in terrestrial and aquatic ecosystems. The continuously expanding databases of fungal genome sequences have been generated by individual and large-scale efforts such as Génolevures [2], Broad Institute's Fungal Genome Initiative, and the 1000 fungal genomes project (<http://1000.fungalgenomes.org>). These efforts have produced a catalog of fungal genes and genomic organization. The genomic datasets can be utilized to better understand how fungi have adapted to their lifestyles and ecological niches. Large datasets of fungal genomic and transcriptomic data have enabled the use of novel methodologies and improved the study of fungal evolution from a molecular sequence perspective [3]. Combined with microscopes, petri dishes, and woodland forays, genome sequencing supports bioinformatics and comparative genomics approaches as important tools in the study of the biology and evolution of fungi.

EVOLUTIONARY RELATIONSHIPS OF FUNGI

Studies of fungal evolution require an understanding of the phylogenetic relationships and relative evolutionary divergence of organisms. The first approaches to organizing fungi into related groups relied on morphological characteristics. These approaches were able to provide a broad framework to organize fungal organisms for taxonomic classification based on recognizable morphological characters such as spore shape, asexual and sexual structures, and in mushroom forming fungi on the shape and presence/absence of gills, veil attachments, and spore color. In zoosporic chytrid fungi the characteristics seen by scanning electron microscopy of zoospores reveal that the ultrastructure of the kinetosomes and flagellum are all diagnostic for the classification of many lineages [4]. However, the microscopic nature of many fungi and especially of yeast-forming fungi with limited visible differences, and the prevalence of convergent evolution to homoplasies or similar characters across a tree, has made taxonomic classification of groups of fungi difficult or easily mislead. The invention and application of DNA sequencing [5], polymerase chain reaction (PCR) [6], and the development of primers to amplify fungal ribosomal RNA (rDNA) enabled a new era of molecular phylogenetic studies in fungi [7]. These approaches provided invaluable information that was used to resolve the major fungal lineages [4,8–22] and the delineation of species [23–26]. Using DNA approaches to study the entire fungal tree of life provided new insight into the order of branching of major groups and the timing of

morphological changes such as the loss of the flagellum found in zoosporic fungi [16,19,20,27].

With improved resolution of the phylogeny of fungal species, the timing of the emergence and changes in species traits and lifestyles can be compared, such as the evolution of host associated symbioses and pathogenic interactions with plants or animals. Analysis of the evolution of morphological complexity along a phylogeny can establish the approximate time when complex growth forms, such as fruiting bodies and multicellular structures, or simplified to unicellular yeast morphology emerged [28]. Changes in subcellular characteristics such as septate hyphae, polarized hyphal growth, and the presence or absence of a flagellated life stage can be mapped on the tree to study the order and timing of their emergence relative to other structures or host associated lifestyles [29,30]. With the availability of genome sequence data, the history of these phenotypic changes can be mapped onto the phylogeny and compared to the evolution of individual genes, presence or absence of a gene family, or correlated with changes in evolutionary rates of gene sequences. These changes may reflect gains but also losses can drive morphological changes such as simplification [28]. The data and approaches are only recently becoming available to support robust analyses to link genes to phenotypes. Some examples of successful applications of the approaches include the acquisition of enzymes needed for anaerobic growth by *Saccharomyces* [31–33], gains of subtilase genes related to animal associated lifestyles [34–36], genome reduction correlated to a yeast growth form [37,38], and changes in structure of centrioles for microtubule attachments [39].

As technology advanced to support inexpensive high-throughput genome sequencing, improved phylogenetic software, and high-performance computing have further improved the resolution of the phylogenetic relationships of fungi (Figure 1). Fungi have been some of the first eukaryotes to benefit from these technological advancements to support the application of phylogenomic methods. Phylogenomics uses multiple orthologous genes, each sampled from a species genome to construct a composite phylogenetic tree from a concatenated dataset or individual gene trees [37,40–44]. A large collection of orthologous loci mined from genome or transcriptome sequences enables phylogenomic studies and tests for conflicting phylogenetic signals. These conflicts may be caused by genomic loci with different evolutionary histories due to, for example, incomplete lineage sorting, horizontal gene transfer, or different selective pressures [41,45–49]. Identification of gene tree and species tree conflicts can help to generate the best representation of the species tree and reveal current or historical selective pressures on genetic loci.

IMPACTS OF ECOLOGICAL NICHE ADAPTATION ON FUNGAL GENOME EVOLUTION

Genome sequencing has enabled comparisons of gene content and sequence changes to begin to predict the likely molecular basis for traits and adaptations. As heterotrophic organisms, fungi obtain carbon and nitrogen from external sources. A variety of cooperative and parasitic associations of fungi with other organisms are found throughout the fungal kingdom. Saprotrophic fungi liberate nutrients by degrading organic matter in habitats

ranging from soils, dead insects and plants, compost piles, animal dung, and water-damaged homes. Ectomycorrhizal (ECM) and arbuscular mycorrhizal (AMF) fungi form mutualistic partnerships with plants and trade plant-produced carbon in the form of sugars in exchange for inorganic nitrogen, phosphorus, iron and other minerals. Fungi can live as commensal associates of plants and animals, for example as plant endophytes or asymptomatic skin fungi, but also can cause devastating diseases in animals and plants via multiple invasive strategies. Some pathogenic fungi produce toxin molecules or effector proteins to kill host cells or disable host defenses while others are opportunistic pathogens that only cause disease when the host becomes sick or immunocompromised.

ECM fungi have mutualistic lifestyles with plants that involve trading resources. Plant pathogens secrete enzymes to break down cell walls. These enzymes can induce a plant defense response [50,51]. Fungi engaged in mutualistic fungal-plant symbioses typically have a reduction in genes encoding enzymes for plant cell wall degradation to avoid eliciting a plant defense response [52]. Instead effectors including small secreted proteins are typically expressed in the ECM fungal-plant interface to establish and promote the two-way partnership [52–54]. AMF fungi also are important plant symbionts contributing to plant health. The molecular components of the interaction and roles of AMF-produced effectors are still emerging areas of research [55,56].

Historical biotic and abiotic interactions have shaped the evolution of genes and the genome organization of fungi. Through the comparison of fungal genomes, the impact of natural selection and neutral processes have been assessed to indicate genes and genomic regions of importance in the evolution of species. For example, wood degrading fungi are classified as brown or white rot fungi depending on their ability to degrade recalcitrant lignin polymers. The woody material in trees and bushes is made up of cellulose and lignin, the latter providing strength to plants. Lignin is highly recalcitrant to degradation and when linked to hemicellulose and cellulose it can be inaccessible to ligninolytic enzymes. To access the lignin, white rot fungi secrete a combination of enzymes and organic acids to break down and later absorb carbohydrate degradation products of cellulose, hemicellulose, and lignin [57]. Comparative analysis of the genomes of brown and white rotters found metabolic and enzymatic gene families varied. The presence of specific families in the brown or white rot species was consistent with their classification and the chemical reactions these fungi can induce to break down woody material [43,58–61]. However, additional analysis have identified that some species of white rot fungi have unexpectedly missing genes that would typically predict they were unable to degrade lignin [62]. Exploration of genomes of two white rot fungi indicated that despite similar lignin degradation capabilities, the species contained different enzyme classes and this suggests that additional pathways of delignification exist and remain to be discovered [63].

Fungi can exist in extreme environments such as the anaerobic rumen stomachs of ruminants [64,65], the dry Atacama Desert in Chile [66,67], hypersaline salterns with NaCl concentrations up to 30% [68], and as endolithic inhabitants of rocks in Antarctica [69,70]. Thermophilic fungi that grow in the desert can survive at temperatures above 60°C [71,72]. Studies of these thermophiles and their genome sequences has led to the development of new enzymes for biotechnology and cell biology studies due to their thermostability [73–

75]. Molecular adaptations that have allowed these fungi to colonize these extreme niches are still being uncovered, and genomic sequencing and comparisons among relatives of extremophiles should provide candidate genes that impact these abilities.

EVOLUTION OF GENOME SIZE

Genome sizes of fungi can vary by almost 3 orders of magnitude. A sampling of 325 phylogenetically diverse fungi has shown that genome sizes vary from 2-Mb in Microsporidia to 2-Gb in Pucciniales fungi with a median of 35 Mb (Data accessed 2017-05-15 from https://github.com/1KFG/genome_stats/; Figure 2). This vast range is the result of multiple genome reduction and expansion events. The total number of predicted protein-coding genes in these fungi varies by an order of magnitude, ranging from 1,800 genes in *Encephalitozoon* (Microsporidia) to 35,000 genes in *Sphaerobolus* (Agaricomycotina), with a median gene count of 11,000 genes. Some of the smallest and most compact genomes can be found in the obligate parasites Microsporidia with sizes in the 2- to 6-Mb range [76–79]. The free living yeasts in the Ascomycota and the Cryptomycota parasite *Rozella* typically have genomes in the 7- to 12-Mb range [80–84] and the Basidiomycota yeasts *Cryptococcus* are around 20 Mb [84–86]. Lineages containing yeast-forming species tend to have smaller genomes (such as *Schizosaccharomyces* and *Ashbya*), but this apparent reduction has occurred independently and multiple times in fungal history [37,38,87].

At the upper end of the range of currently sequenced species are the 150 to 175-Mb genomes of *Cenococcum geophilum* (Dothidiomycetes; Ascomycota), *Sphaerobolus stellatus* (Agaricomycotina; Basidiomycota), *Tuber melanosporum* (Pezizales; Ascomycota), and *Blumeria graminis* (Leotiomycetes; Ascomycota) [52,88–90], which are primarily plant-associated fungi with both biotrophic and mutualistic lifestyles. Genome expansions in these species appear to have been driven mostly by transposon element content expansion. The total gene count is also higher in these genomes, which may belie an increase in gene duplication or insertion events that accompany the evolutionary processes that enabled increased transposon copy number.

Genomes of Entomophthoromycotina (Zoopagomycota) also are extremely large. The genome of *Entomophaga aulicae* is estimated to be as large as 8 Gb based on estimates using nuclear staining approaches [91], though sequencing has not yet been attempted. The genomes of the insect-killing zygomycete fungi *Entomophthora muscae* and *Zoophthora radicans* (Entomophthoromycotina; Zoopagomycota) appear to be in the ~700-Mb to 1.5-Gb range based on sequencing done through the Joint Genome Institute for the 1000 Genomes project and others (MB Eisen and H. de Fine Licht *personal communication*). The large genome size appears to be driven by increases in transposable elements, while gene count is not substantially expanded based on RNA-seq of these and related species [92,93]. Genome size estimation using flow cytometry has indicated that many of the rust fungi (Pucciniales; Pucciniomycotina) also have large genomes with estimated sizes of 300 to 900 Mb [94].

Genome reduction has also occurred in several fungal lineages, with the highly reduced genomes of the obligate parasitic Microsporidian fungi being some of the most prominent

examples with tiny genomes (by fungal standards) in the 2- to 6-Mb range [76–79]. However, not all Microsporidia have tiny genomes; some are in the 16- to 20-Mb range, which seems to be due to transposon insertions in the few cases that have been examined [95]. A smaller genome lends itself to fewer genes; as such Microsporidia have a highly reduced gene set, dispensing with most small molecule production and energy production pathways in favor of uptake transporters to obtain these resources from hosts [79,96–98]. In addition to fewer genes, the length of gene sequences themselves are reduced as the selective pressures that resulted in reduced genomes size also contributed to reduced gene length [77,96,99]. Coding space is at such a premium, with genes found nearly every 1,000 bp in some species [76], that some transcribed genes overlap [99,100]. Other obligate parasites in the fungal kingdom such as *Pneumocystis* demonstrate reduced genomes in the 8-Mb range with approximately 3,700 genes [101–103] suggesting the presence of common selective pressures to reduce genome size as part of a tight host association in some parasitic fungal-host interactions.

Reduced genomes are a hallmark of yeast-forming lineages. Prominent examples include the Saccharomycotina yeast *Ashbya gossypii* with a 9-Mb genome and 5,300 genes and the Taphrinomycotina fungus *Schizosaccharomyces pombe*, also known as fission yeast, with a 12-Mb genome and 5,100 genes [81,87,104]. The fern pathogen *Mixia osmundae* (Pucciniomycotina; Basidiomycota) has a 14-Mb genome [83] and 7,000 genes and the human pathogenic *Cryptococcus* yeasts (Tremellomycetes; Basidiomycota) [84–86] have 19-Mb genomes with around 7,000 protein coding genes. In each of these clades of yeast-forming fungi the genome sizes tend to be smaller than their filamentous sister clades. The filamentous Pezizomycotina filamentous fungi, sister to the Saccharomycetales yeasts, have genomes in the 35- to 45-Mb range and the Agaricomycotina fungi sister to the Pucciniomycotina are typically in the 45- to 60-Mb range. Analyses of gene gain and loss in yeast lineages have revealed that major gene losses occurred in the evolutionary history of these lineages indicating genome reduction in the transition to single-celled growth [37,38,87].

Efforts to study how changes in gene content and evolution affect different lineages have identified classes of genes and genomic regions that change at different rates [105,106]. Within a genome, gene family copy number dynamics, transposable element transposition frequency, and individual gene evolution varies across a genome which could be a consequence of different selective pressures but also influenced random genetic drift. An important driver in the importance of random genetic drift vs selection in shaping a genome is the effective population size (N_e) of a species. An organism's mode of dispersal, outcrossing frequency, rapidity of cell division can all influence N_e though the driving factors that determine effective population size are not well explored in fungi. Some of these regions, like effectors and defense genes, can be important pathogenic or symbiosis associated genes. The processes that establish and maintain different rates of change are likely not universal but genome regions with extremely high rates of molecular evolution are particularly common in plants, fungi and oomycete species [107–112] and may be important sources for novelty within species.

Many of the studies of genome size change are limited to lineages that diverged many millions of years ago. This divergence does not allow for the study of the mechanisms of genome size changes occurring at the population level. While aneuploidy and polyploidy manipulation or large scale acquisition of DNA has been explored in *Saccharomyces* [113–116], studies of recent changes in genome size by massive gene duplications or transposon proliferation could reveal fitness consequences and the relative role of neutral vs directional selection in the success of lineages with genome size expansions [117,118]. Increased genome size may also result from changes in effective population sizes leading to relaxed selection and genome size increase [117]. What might drive changes in population sizes? A newly acquired plant-associated lifestyle may impose constraints on reproductive modes (eg timing and availability of partners) or dispersal (eg, how spores are produced). A better understanding of the pressures that drive genome size change could help us to understand how demography and transposable element proliferation influence fungal evolution, and in some cases how they have enabled the emergence of many disease-causing plant pathogens.

Gene and Gene Family Size Dynamics

Sampling entire genomes has allowed for increased resolution regarding the relationships between fungal lineages as well as the history of individual genes. Reconstruction of individual trees for each gene in the genome can provide a means to establish the age and coalescent history of a gene eg, a gene could originate with the Eukaryotes, in the Animal-Fungi ancestor, or be fungal-specific. Tools such as PhylomeDB and Ensembl Genomes Compara provide interfaces to explore these reconstructions to understand the history of a single gene [119,120]. Other events that generate copy number expansions of a gene or gene family through duplication can be identified, and the timing of these duplication events can be established when comparing copy number of the same gene family across a phylogeny of species with sequenced genomes. Likewise, a comparison of gene family contractions and gene losses can be studied to identify when potential function or diversity was lost. These changes in genome content provide important insights into adaptations that organisms may experience due to shifts in ecological niches or associations with a plant or animal hosts.

Gene family expansions

Comparisons of gene families between species have revealed several instances of gene copy number expansions possibly driven by evolutionary adaptations; such expansions have been instrumental in the evolution of pathogenicity traits. Copy number expansions of fungal genes containing the carbohydrate-binding LysM motif have been documented in both animal and plant pathogens [121–124]. LysM protein motifs bind chitin or chitin-like carbohydrates and peptidoglycans [121,125] and their role in fungi may be to bind the chitin in fungal cell walls to avoid triggering recognition by the plant or animal host defenses [126]. Expanded copy number of these genes and the domain may be a signature of species that have biotrophic interactions with a host and recent expansions could indicate a recent shift to this association from a saprotrophic lifestyle. The genomes of the human pathogenic fungi and basidiomycete yeasts *Cryptococcus neoformans* and *C. gattii* show expansions of sugar and major facilitator superfamily genes [84,85] hypothesized to play a role in increased uptake of these molecules from the environment [127] and could be important in

synthesis and transport of the prominent capsule that is composed of the polysaccharides glucuronoxylomannan and glucuronoxylomannogalactan [128–130].

Expansion of the subtilase and metalloproteases gene families have also been noted as important in the transition to an animal pathogenic lifestyle in the filamentous ascomycetes Onygenales [34,36,131]. The M36 metalloprotease family has expanded in *Coccidioides* fungi and their close relatives and is hypothesized to be linked to the switch from plant to animal associated ecologies and the switch from obtaining nutrients from plant-based carbohydrates to animal keratin and proteins [34,35,132]. Research in animal-associated dermatophyte fungi has revealed similar, but typically independent, expansions of proteases in *Blastomyces* [133], *Trichophyton* and *Microsporum* [124]. Interestingly, the human pathogen *Sporothrix*, not an Onygenales fungi but a member of a different clade (Ophiostomataceae; Sordariomycete), does not show signatures of recent protease family expansion, suggesting a different transition to mammalian association.

Comparison of the genes in the amphibian disease causing chytrid fungus *Batrachochytrium dendrobatidis* (Bd) to a non-pathogenic relative also identified expansions within protease families [134]. The copy number of aspartyl and multiple metalloprotease gene families and the chitin binding domain CBM18 are dramatically expanded in the pathogen as compared to non-pathogenic sister species [134]. The importance of these expansions in pathogenesis is suggested by several investigations. One study found that a subtilisin-like serine protease was upregulated in response to amphibian host expression of thyroid hormone necessary for amphibian development [135]. The CBM18 gene has the highest copy number of any fungus, ranging from 65-90 copies among sequenced strains, and has been under recent positive selection indicating it may be an important contributor to its pathogenicity [136,137]. Cloning and expression of the domain demonstrated that it also is capable of binding chitin [138]. Comparison with the closest relative, *B. salamandrivorans*, also a successful and recently emerging pathogen, supports a hypothesis that the timing of these protease and CBM18 gene family expansions coincide with the emergence of the two *Batrachochytrium* lineages [137].

Plant pathogenic fungi have also undergone gene copy number expansion effectively enabling host colonization and the ability to overcome plant defenses. One example is secreted effector proteins, which are expanded and diversifying in rust genomes (Pucciniomycotina; Basidiomycota) [139]. Recent transposable element expansion, which is associated with gene duplications and accelerated rates of effector gene evolution, is noted in *Leptosphaeria maculans* (Pleosporales; Dothideomycetes) [107,111]. Other members of the *L. maculans* species complex have small genomes and lack this genome expansion. The powdery mildew *Blumeria graminis* has a large genome with an expansion of atypical avirulence genes and signal peptide-containing genes [90]. Metalloproteases and alpha amylases are expanded in the important plant disease-causing fungus *Zymoseptoria tritici* (formerly *Mycosphaerella graminicola*) (Capnodiales; Dothideomycetes). In contrast contraction of CAZy family genes in *Z. tritici* suggest a specialization on the types of carbon sources utilized for nutrition [140].

Recent gene gains and losses have occurred during the evolution of insect-associated fungi, and these changes appear to impact host specificity. The transition between generalist and specialist in *Metarhizium* species may have been driven by gene family contractions [141,142]. The “domesticated” fungus cultivated by leaf cutter ants, *Leucoagaricus gongylophorus*, has an expansion of CAZymes related to polysaccharide degradation. These enzymes are differentially expressed depending on the plant substrates ‘fed’ to the fungus garden by leaf cutter farming ants [143–149]. The specialized gongylidia that are swellings of the hyphal tip have evolved to provide a sugar nutrient source for the ants in exchange for the the input of leaf and plant material into the fungal garden. The expansion and specialization of the fungal enzyme families necessary for rapid extraction of carbohydrates from plant material has likely been driven by this highly mutualistic symbiosis [147–149].

Expansions are not always linked to pathogenicity. The extensive light responsive nature of the zygomycete *Phycomyces blakesleeanus* (Mucoromycotina; Mucoromycota) is likely the result of the expansion of signaling pathways [150]. These signaling protein expansions are also seen in the relatively closely related species *Rhizopus delemar* (previously identified as *Rhizopus oryzae*) [151] which may have enabled these coprophilic fungi to optimize the timing of fruiting and spore maturation in sync with the ephemeral ecology of a dung. Producing and orienting spore forming structures at the right time of day can maximize the probability that offspring will be dispersed and establish the next generation. Genes encoding hydrophobin proteins, which are important for fruiting body development in mushrooms, are also expanded in copy number in Agaricomycotina species [152–155]. The p450 monooxygenase family is also highly expanded in mushroom-forming fungi, especially in white rot fungi such as *Phanerochaete*, which likely allow it to degrade a rich collection of substrates including lignin [63,152,156]. These expansions may have been important in niche adaptations and the evolution of specific traits such as lignin modifications and degradation, decomposition of complex hydrocarbons, and the ability to growth as a biotrophic plant pathogen [157–163].

Gene family contractions

Gene family contraction and gene loss have contributed to the evolution of fungal genomes. Some of these changes can be correlated to recent shifts in ecology while other analyses have revealed ancient changes that appear to underlie a simplification in growth morphology. Researchers undertook a comparative analysis of 59 fungal genomes and examined changes in gene families corresponding to 5 independent lineages that grow primarily as single-cell yeast forms. The analysis used a newly developed method called COMPARE (comparative phylogenomic analysis of trait evolution) to infer that evolution of yeast growth forms occurred by convergent evolutionary processes leading to parallel, independent gene family losses [37]. The predominant pattern of observed losses were in plant cell wall degrading enzymes, fungal lysozymes, p450 families, and cyclophilins that serve as molecular chaperones.

Gene family contractions are evident in the plant pathogen *Colletotrichum* (Glomerellales; Sordariomycetes) and are associated with host range contractions [164] suggesting that host specificity may be a result of gene losses. Extensive gene losses were noted in the genome of

Escovopsis weberi, an ascomycete pathogen of the *Leucoagaricus* ant-farmed basidiomycete fungi. These extensive gene losses in this species could result from specialization to mycoparasitism [165]. Gene family contractions are not seen in the related mycoparasitic *Trichoderma sp.*, suggesting a different route of host specialization in *Escovopsis*. Loss of gene families, such as of dehydrogenases, have been documented in the insect pathogens *Metarhizium* and interpreted to reflect adaptation to host specificity [142].

A lack of duplicate genes is not always a direct result of gene loss. In species in which repeat-induced point mutation (RIP) occurs, gene duplications cannot persist because RIP, a genome defense mechanism, targets duplicated sequences so that they accumulate point mutations during the meiotic cycle [166,167]. RIP is hypothesized to be a potent defense against transposable element proliferation because both the source and transposed copy of an element will become mutated. The genome of the ascomycete *Neurospora crassa* has been shaped by RIP. *N. crassa* does not have a reduced genome (40 Mb, ~10,000 genes), but lacks nearly any active transposable elements but also does not have any large gene families [168,169].

GENOME STABILITY AND PAN-GENOMES

Gene content and genome copy number can vary, sometimes dramatically, in a population and across a species. Sequenced genomes represent a snapshot of the genomic information of a species or strain. The inventory of genes revealed by sequencing can be useful when comparing between isolates or sampling a population of individuals at different times. Changes in genomic content can occur among individuals in a population or even within a strain over time. Considering the complete set of genes across all strains or individuals of a species is deemed the pan-genome [170] which can be useful way to think about not just gene presence/absence compared to a “reference” but the complete set of genes that exists in a species or a collection individuals [171]. Genetic variation includes single nucleotide substitutions, insertion/deletions, or larger genetic content changes such as transposable elements and transposition events. The presence (1), absence (0), or amplification of copy number (> 1 copies) a gene can also be evaluated among individuals in a population. Together these approaches can rank and identify fast or slow evolving genes and evaluate the evolutionary lability of genes and pathways which could underlie changes in function among populations and species.

Investigations have revealed that gene content and genome copy number can vary, sometimes dramatically, in a population and across a species. In *Saccharomyces cerevisiae*, completed genomes of 100 individual strains have been used to generate a pan-genome of fungal genes, some of which are present in some but not all strains [172]. Changes are more common, but not exclusive to subtelomeric regions of chromosomes. Variation in the tempo and mode of chromosomal rearrangements and gene shuffling can be seen in wild and domesticated species when comparing *S. cerevisiae* and *Saccharomyces paradoxus* [173] and wild or domesticated *Aspergillus* strains [174,175]. The human pathogen *C. gattii* has genomic segments that vary in copy number, segregate in the population, and could be a contributing mechanism to virulence differences among strains [86,176].

The importance of genome variation at the population level is also appreciated in plant pathogenic fungi where variation in virulence and prevalence from year to year can sometimes be linked to a single gene or to changes in chromosome content. Genes encoded on dispensable chromosomes are sources of rapid changes in gene content as these chromosomes can be transferred between individual strains and often lost without disruption of primary metabolic or cellular functions [177–179]. Also known as accessory chromosomes, these may accumulate transposable elements and evolve more quickly than other chromosomes because they typically do not encode essential genes [109,180]. These chromosomes further support a mechanism of gaining or losing sets of genes that may be important in adaptation to new host plants [179]. The relative importance and molecular mechanism impacted by these genetic elements in modulating adaptability of species remains to be explored but can be important contributors to the timing and genome evolution.

Conclusions

Complete sequencing of fungal genomes has enabled comparisons of the dynamic genome size and gene content across a range of time in fungal evolution. Genome differences that are also identified through comparative genomics can help to form hypotheses about molecular mechanisms for adaptation to new ecological niches or fungal-host specialization. These identified changes establish guides for further genetic and molecular biology experimentation. Genome content comparisons also highlight the relative lability of fungal processes: core metabolism changes little, but copy number of transcription factors, secondary metabolites, and transporter families ebb and wane across the kingdom. Sequencing and analysis tools have permitted the detailed cataloging of where and how much change occurs across genomes, providing rationale for molecular experiments to study the functions of the genes implicated.

References

1. Stajich JE , Berbee ML , Blackwell M , Hibbett DS , James TY , Spatafora JW , Taylor JW . The fungi. *Curr Biol.* 2009 9 29;19(18):R840–5.19788875
2. Sherman D , Durrens P , Beyne E , Nikolski M , Souciet J-L , Génolevures Consortium. Genolevures: comparative genomics and molecular evolution of hemiascomycetous yeasts. *Nucleic Acids Res.* 2004 1 1;32(Database issue):D315–8.14681422
3. Hibbett DS , Stajich JE , Spatafora JW . Toward genome-enabled mycology. *Mycologia.* 2013 8 8;105(6):1339–49.23928422
4. James TY , Letcher PM , Longcore JE , Mozley-Standridge SE , Porter D , Powell MJ , Griffith GW , Vilgalys R . A molecular phylogeny of the flagellated fungi (Chytridiomycota) and description of a new phylum (Blastocladiomycota). *Mycologia.* 2006 11;98(6):860–71.17486963
5. Sanger F , Nicklen S , Coulson AR . DNA sequencing with chain-terminating inhibitors. *Proceedings of the National Academy of Sciences.* 1977 12 1;74(12):5463–7.
6. Saiki RK , Gelfand DH , Stoffel S , Scharf SJ , Higuchi R . Primer-Directed Enzymatic Amplification of DNA with a Thermostable DNA Polymerase. *Science; Washington* 1988 1 29;239(4839):487–92.2448875
7. White TJ , Bruns TD , Lee S , Taylor J . Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics In: Innis MA , Gelfand D , Sninsky J , T.J. W , editors. *PCR Protocols: A Guide to Methods and Applications.* New York, USA: Academic Press; 1990 p. 315–22.

8. Bruns TD , Vilgalys R , Barns SM , Gonzalez D , Hibbett DS , Lane DJ , Simon L , Stickel S , Szaro TM , Weisburg WG , Sogin ML . Evolutionary relationships within the fungi: Analyses of nuclear small subunit rRNA sequences - ScienceDirect. *Mol Phylogenet Evol.* 1992;1(3):231–41.1342940
9. Kurtzman CP . Molecular taxonomy of the yeasts. *Yeast.* 1994 12;10(13):1727–40.7747515
10. Spatafora JW , Mitchell TG , Vilgalys R . Analysis of genes coding for small-subunit rRNA sequences in studying phylogenetics of dematiaceous fungal pathogens. *J Clin Microbiol.* 1995 5;33(5):1322–6.7615749
11. Moncalvo JM , Lutzoni FM , Rehner SA , Johnson J , Vilgalys R . Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Syst Biol.* 2000 6;49(2):278–305.12118409
12. Moncalvo JM , Vilgalys R , Redhead SA , Johnson JE , James TY , Catherine Aime M , Hofstetter V , Verduin SJ , Larsson E , Baroni TJ , Greg Thorn R , Jacobsson S , Clemencon H , Miller OK . One hundred and seventeen clades of euagarics. *Mol Phylogenet Evol.* 2002;23:357–400.12099793
13. O'Donnell K , Lutzoni FM , Ward TJ , Benny GL . Evolutionary Relationships among Mucoralean Fungi (Zygomycota): Evidence for Family Polyphyly on a Large Scale. *Mycologia.* 2001 3 1;93(2):286–97.
14. Redecker D , Raab P . Phylogeny of the glomeromycota (arbuscular mycorrhizal fungi): recent developments and new gene markers. *Mycologia.* 2006 11;98(6):885–95.17486965
15. Spatafora JW , Sung G-H , Johnson D , Hesse C , O'Rourke B , Serdani M , Spotts R , Lutzoni F , Hofstetter V , Miadlikowska J , Reeb V , Gueidan C , Fraker E , Lumbsch T , Lücking R , Schmitt I , Hosaka K , Aptroot A , Roux C , Miller AN , Geiser DM , Hafellner J , Hestmark G , Arnold AE , Budel B , Rauhut A , Hewitt D , Untereiner WA , Cole MS , Scheidegger C , Schultz M , Sipman H , Schoch CL . A five-gene phylogeny of Pezizomycotina. *Mycologia.* 2006 11;98(6):1018–28.17486977
16. James TY , Kauff F , Schoch CL , Matheny PB , Hofstetter V , Cox CJ , Celio G , Gueidan C , Fraker E , Miadlikowska J , Lumbsch HT , Rauhut A , Reeb V , Arnold AE , Amtoft A , Stajich JE , Hosaka K , Sung GH , Johnson D , O'Rourke B , Crockett M , Binder M , Curtis JM , Slot JC , Wang Z , Wilson AW , Schussler A , Longcore JE , O'Donnell K , Mozley-Standridge S , Porter D , Letcher PM , Powell MJ , Taylor JW , White MM , Griffith GW , Davies DR , Humber RA , Morton JB , Sugiyama J , Rossman AY , Rogers JD , Pfister DH , Hewitt D , Hansen K , Hambleton S , Shoemaker RA , Kohlmeyer J , Volkmann-Kohlmeyer B , Spotts RA , Serdani M , Crous PW , Hughes KW , Matsuura K , Langer E , Langer G , Untereiner WA , Lücking R , Budel B , Geiser DM , Aptroot A , Diederich P , Schmitt I , Schultz M , Yahr R , Hibbett DS , Lutzoni F , McLaughlin DJ , Spatafora JW , Vilgalys R . Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature.* 2006;443:818–22.17051209
17. Suh S-O , Blackwell M , Kurtzman CP , Lachance M-A . Phylogenetics of Saccharomycetales, the ascomycete yeasts. *Mycologia.* 2006 11;98(6):1006–17.17486976
18. White MM , James TY , O'Donnell K , Cafaro MJ , Tanabe Y , Sugiyama J . Phylogeny of the Zygomycota based on nuclear ribosomal sequence data. *Mycologia.* 2006 11;98(6):872–84.17486964
19. McLaughlin DJ , Hibbett DS , Lutzoni F , Spatafora JW , Vilgalys R . The search for the fungal tree of life. *Trends Microbiol.* 2009 11;17(11):488–97.19782570
20. Schoch CL , Sung GH , Lopez-Giraldez F , Townsend JP , Miadlikowska J , Hofstetter V , Robbertse B , Matheny PB , Kauff F , Wang Z , Gueidan C , Andrie RM , Trippe K , Ciuffetti LM , Wynns A , Fraker E , Hodkinson BP , Bonito G , Groenewald JZ , Arzanlou M , de Hoog GS , Crous PW , Hewitt D , Pfister DH , Peterson K , Gryzenhout M , Wingfield MJ , Aptroot A , Suh SO , Blackwell M , Hillis DM , Griffith GW , Castlebury LA , Rossman AY , Lumbsch HT , Lücking R , Budel B , Rauhut A , Diederich P , Ertz D , Geiser DM , Hosaka K , Inderbitzin P , Kohlmeyer J , Volkmann-Kohlmeyer B , Mostert L , O'Donnell K , Sipman H , Rogers JD , Shoemaker RA , Sugiyama J , Summerbell RC , Untereiner W , Johnston PR , Stenroos S , Zuccaro A , Dyer PS , Crittenden PD , Cole MS , Hansen K , Trappe JM , Yahr R , Lutzoni F , Spatafora JW . The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Syst Biol.* 2009;58:224–39.20525580

21. Wang Y , Tretter ED , Johnson EM , Kandel P , Lichtwardt RW , Novak SJ , Smith JF , White MM . Using a five-gene phylogeny to test morphology-based hypotheses of Smittium and allies, endosymbiotic gut fungi (Harpellales) associated with arthropods. *Mol Phylogenet Evol.* 2014 10;79:23–41.24933275
22. Porter TM , Martin W , James TY , Longcore JE , Gleason FH , Adler PH , Letcher PM , Vilgalys R . Molecular phylogeny of the Blastocladiomycota (Fungi) based on nuclear ribosomal DNA. *Fungal Biol.* 2011 4;115(4–5):381–92.21530920
23. Taylor JW , Jacobson DJ , Kroken S , Kasuga T , Geiser DM , Hibbett DS , Fisher MC . Phylogenetic Species Recognition and Species Concepts in Fungi. *Fungal Genet Biol.* 2000 10 1;31(1):21–32.11118132
24. Taylor JW , Turner E , Townsend JP , Dettman JR , Jacobson D . Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philos Trans R Soc Lond B Biol Sci.* 2006 11 29;361(1475):1947–63.17062413
25. Dettman JR , Jacobson DJ , Taylor JW . Multilocus sequence data reveal extensive phylogenetic species diversity within the *Neurospora discreta* complex. *Mycologia.* 2006 5;98(3):436–46.17040072
26. Vialle A , Feau N , Frey P , Bernier L , Hamelin RC . Phylogenetic species recognition reveals host-specific lineages among poplar rust fungi. *Mol Phylogenet Evol.* 2013/3;66(3):628–44.23147268
27. Hibbett DS , Binder M , Bischoff JF , Blackwell M , Cannon PF , Eriksson OE , Huhndorf S , James T , Kirk PM , Lücking R , Thorsten Lumbsch H , Lutzoni F , Matheny PB , McLaughlin DJ , Powell MJ , Redhead S , Schoch CL , Spatafora JW , Stalpers JA , Vilgalys R , Aime MC , Aptroot A , Bauer R , Begerow D , Benny GL , Castlebury LA , Crous PW , Dai Y-C , Gams W , Geiser DM , Griffith GW , Gueidan C , Hawksworth DL , Hestmark G , Hosaka K , Humber RA , Hyde KD , Ironside JE , Køljalg U , Kurtzman CP , Larsson K-H , Lichtwardt R , Longcore J , Miadlikowska J , Miller A , Moncalvo J-M , Mozley-Standridge S , Oberwinkler F , Parmasto E , Reeb V , Rogers JD , Roux C , Ryvarden L , Sampaio JP , Schüssler A , Sugiyama J , Thorn RG , Tibell L , Untereiner WA , Walker C , Wang Z , Weir A , Weiss M , White MM , Winka K , Yao Y-J , Zhang N . A higher-level phylogenetic classification of the Fungi. *Mycol Res.* 2007 5;111 (Pt 5):509–47.17572334
28. O'Malley MA , Wideman JG , Ruiz-Trillo I . Losing Complexity: The Role of Simplification in Macroevolution. *Trends Ecol Evol.* 2016 8;31(8):608–21.27212432
29. Celio GJ , Padamsee M , Dentinger BTM , Bauer R , McLaughlin DJ . Assembling the Fungal Tree of Life: constructing the structural and biochemical database. *Mycologia.* 2006 11;98(6):850–9.17486962
30. Kumar TKA , Crow JA , Wennblom TJ , Abril M , Letcher PM , Blackwell M , Roberson RW , McLaughlin DJ . An ontology of fungal subcellular traits. *Am J Bot.* 2011 9;98(9):1504–10.21875969
31. Hall C , Dietrich FS . The reacquisition of biotin prototrophy in *Saccharomyces cerevisiae* involved horizontal gene transfer, gene duplication and gene clustering. *Genetics.* 2007;177:2293–307.18073433
32. Gojkovic Z , Knecht W , Zameitat E , Warneboldt J , Coutelis JB , Pynyaha Y , Neuveglise C , Moller K , Löffler M , Piskur J . Horizontal gene transfer promoted evolution of the ability to propagate under anaerobic conditions in yeasts. *Mol Genet Genomics.* 2004;271:387–93.15014982
33. Piskur J , Rozpedowska E , Polakova S , Merico A , Compagno C . How did *Saccharomyces* evolve to become a good brewer? *Trends Genet.* 2006;22:183–6.16499989
34. Sharpton TJ , Stajich JE , Rounsley SD , Gardner MJ , Wortman JR , Jordar VS , Maiti R , Kodira CD , Neafsey DE , Zeng Q , Hung C-Y , McMahan C , Muszewska A , Grynberg M , Mandel MA , Kellner EM , Barker BM , Galgiani JN , Orbach MJ , Kirkland TN , Cole GT , Henn MR , Birren BW , Taylor JW . Comparative genomic analyses of the human fungal pathogens *Coccidioides* and their relatives. *Genome Res.* 2009 10;19(10):1722–31.19717792
35. Whiston E , Taylor JW . Comparative Phylogenomics of Pathogenic and Nonpathogenic Species. *G3.* 2015 11 27;6(2):235–44.
36. Muszewska A , Taylor JW , Szczesny P , Grynberg M . Independent Subtilases Expansions in Fungi Associated with Animals. *Mol Biol Evol.* 2011 12 1;28(12):3395–404.21727238

37. Nagy LG , Ohm RA , Kovács GM , Floudas D , Riley R , Gácsér A , Sipiczki M , Davis JM , Doty SL , de Hoog GS , Lang BF , Spatafora JW , Martin FM , Grigoriev IV , Hibbett DS . Latent homology and convergent regulatory evolution underlies the repeated emergence of yeasts. *Nat Commun.* 2014 7 18;5:4471.25034666
38. Nguyen TA , Cissé OH , Yun Wong J , Zheng P , Hewitt D , Nowrousian M , Stajich JE , Jedd G . Innovation and constraint leading to complex multicellularity in the Ascomycota. *Nat Commun.* 2017 2 8;8:14444.
39. Carvalho-Santos Z , Machado P , Branco P , Tavares-Cadete F , Rodrigues-Martins A , Pereira-Leal JB , Bettencourt-Dias M . Stepwise evolution of the centriole-assembly pathway. *J Cell Sci.* 2010 5 1;123(Pt 9):1414–26.20392737
40. Wapinski I , Pfeffer A , Friedman N , Regev A . Natural history and evolutionary principles of gene duplication in fungi. *Nature.* 2007 9 6;449(7158):54–61.17805289
41. Fitzpatrick DA , Logue ME , Stajich JE , Butler G . A fungal phylogeny based on 42 complete genomes derived from supertree and combined gene analysis. *BMC Evol Biol.* 2006 11 22;6:99.17121679
42. Gibbons JG , Janson EM , Hittinger CT , Johnston M , Abbot P , Rokas A . Benchmarking next-generation transcriptome sequencing for functional and evolutionary genomics. *Mol Biol Evol.* 2009 12;26(12):2731–44.19706727
43. Floudas D , Binder M , Riley R , Barry K , Blanchette RA , Henrissat B , Martinez AT , Otillar R , Spatafora JW , Yadav JS , Aerts A , Benoit I , Boyd A , Carlson A , Copeland A , Coutinho PM , de Vries RP , Ferreira P , Findley K , Foster B , Gaskell J , Glotzer D , Gorecki P , Heitman J , Hesse C , Hori C , Igarashi K , Jurgens JA , Kallen N , Kersten P , Kohler A , Kues U , Kumar TK , Kuo A , LaButti K , Larrondo LF , Lindquist E , Ling A , Lombard V , Lucas S , Lundell T , Martin R , McLaughlin DJ , Morgenstern I , Morin E , Murat C , Nagy LG , Nolan M , Ohm RA , Patyshakuliyeva A , Rokas A , Ruiz-Duenas FJ , Sabat G , Salamov A , Samejima M , Schmutz J , Slot JC , St John F , Stenlid J , Sun H , Sun S , Syed K , Tsang A , Wiebenga A , Young D , Pisabarro A , Eastwood DC , Martin F , Cullen D , Grigoriev IV , Hibbett DS . The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science.* 2012;336:1715–9.22745431
44. Spatafora JW , Chang Y , Benny GL , Lazarus K , Smith ME , Berbee ML , Bonito G , Corradi N , Grigoriev I , Gryganskyi A , James TY , O'Donnell K , Roberson RW , Taylor TN , Uehling J , Vilgalys R , White MM , Stajich JE . A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia.* 2016 9;108(5):1028–46.27738200
45. Reeb V , Lutzoni F , Roux C . Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phylogenet Evol.* 2004/9;32(3):1036–60.15288074
46. Moncalvo J-M , Nilsson RH , Koster B , Dunham SM , Bernauer T , Matheny PB , Porter TM , Margaritescu S , Weiß M , Garnica S , Danell E , Langer G , Langer E , Larsson E , Larsson K-H , Vilgalys R . The Cantharelloid Clade: Dealing with Incongruent Gene Trees and Phylogenetic Reconstruction Methods. *Mycologia.* 2006;98(6):937–48.17486970
47. Strandberg R , Nygren K , Menkis A , James TY , Wik L , Stajich JE , Johannesson H . Conflict between reproductive gene trees and species phylogeny among heterothallic and pseudohomothallic members of the filamentous ascomycete genus *Neurospora*. *Fungal Genet Biol.* 2010 10;47(10):869–78.20601044
48. Salichos L , Rokas A . Inferring ancient divergences requires genes with strong phylogenetic signals. *Nature.* 2013;497:327–31.23657258
49. Salichos L , Stamatakis A , Rokas A . Novel information theory-based measures for quantifying incongruence among phylogenetic trees. *Mol Biol Evol.* 2014 5;31(5):1261–71.24509691
50. Bradley DJ , Kjellbom P , Lamb CJ . Elicitor- and wound-induced oxidative cross-linking of a proline-rich plant cell wall protein: a novel, rapid defense response. *Cell.* 1992 7 10;70(1):21–30.1623521
51. Lamb CJ , Lawton MA , Dron M , Dixon RA . Signals and transduction mechanisms for activation of plant defenses against microbial attack. *Cell.* 1989 1 27;56(2):215–24.2643475

52. Kohler A , Kuo A , Nagy LG , Morin E , Barry KW , Buscot F , Canbäck B , Choi C , Cichocki N , Clum A , Colpaert J , Copeland A , Costa MD , Doré J , Floudas D , Gay G , Girlanda M , Henrissat B , Herrmann S , Hess J , Högborg N , Johansson T , Khouja H-R , LaButti K , Lahrmann U , Levasseur A , Lindquist EA , Lipzen A , Marmeisse R , Martino E , Murat C , Ngan CY , Nehls U , Plett JM , Pringle A , Ohm RA , Perotto S , Peter M , Riley R , Rineau F , Ruytinx J , Salamov A , Shah F , Sun H , Tarkka M , Tritt A , Veneault-Fourrey C , Zuccaro A , Mycorrhizal Genomics Initiative Consortium, Tunlid A , Grigoriev IV , Hibbett DS , Martin F . Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nat Genet.* 2015 4;47(4):410–5.25706625
53. Martin F , Aerts A , Ahrén D , Brun A , Danchin EGJ , Duchaussoy F , Gibon J , Kohler A , Lindquist E , Pereda V , Salamov A , Shapiro HJ , Wuyts J , Blaudez D , Buée M , Brokstein P , Canbäck B , Cohen D , Courty PE , Coutinho PM , Delaruelle C , Detter JC , Deveau A , DiFazio S , Duplessis S , Fraissinet-Tachet L , Lucic E , Frey-Klett P , Fourrey C , Feussner I , Gay G , Grimwood J , Hoegger PJ , Jain P , Kilaru S , Labbé J , Lin YC , Legué V , Le Tacon F , Marmeisse R , Melayah D , Montanini B , Muratet M , Nehls U , Niculita-Hirzel H , Oudot-Le Secq MP , Peter M , Quesneville H , Rajashekar B , Reich M , Rouhier N , Schmutz J , Yin T , Chalot M , Henrissat B , Kües U , Lucas S , Van de Peer Y , Podila GK , Polle A , Pukkila PJ , Richardson PM , Rouzé P , Sanders IR , Stajich JE , Tunlid A , Tuskan G , Grigoriev IV . The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. *Nature.* 2008 3 6;452(7183):88–92.18322534
54. Plett JM , Kemppainen M , Kale SD , Kohler A , Legué V , Brun A , Tyler BM , Pardo AG , Martin F . A Secreted Effector Protein of *Laccaria bicolor* Is Required for Symbiosis Development. *Curr Biol.* 2011 7 26;21(14):1197–203.21757352
55. Kloppeholz S , Kuhn H , Requena N . A Secreted Fungal Effector of *Glomus intraradices* Promotes Symbiotic Biotrophy. *Curr Biol.* 2011 7 26;21(14):1204–9.21757354
56. S dzielewska Toro K , Brachmann A . The effector candidate repertoire of the arbuscular mycorrhizal fungus *Rhizophagus clarus*. *BMC Genomics.* 2016;17(1): 101.26861502
57. Dashtban M , Schraft H , Syed TA , Qin W . Fungal biodegradation and enzymatic modification of lignin. *Int J Biochem Mol Biol.* 2010;1(1):36–50.21968746
58. Eastwood DC , Floudas D , Binder M , Majcherzyk A , Schneider P , Aerts A , Asiegbu FO , Baker SE , Barry K , Bendiksby M , Blumentritt M , Coutinho PM , Cullen D , de Vries RP , Gathman A , Goodell B , Henrissat B , Ihrmark K , Kauserud H , Kohler A , LaButti K , Lapidus A , Lavin JL , Lee YH , Lindquist E , Lilly W , Lucas S , Morin E , Murat C , Oguiza JA , Park J , Pisabarro AG , Riley R , Rosling A , Salamov A , Schmidt O , Schmutz J , Skrede I , Stenlid J , Wiebenga A , Xie X , Kües U , Hibbett DS , Hoffmeister D , Högborg N , Martin F , Grigoriev IV , Watkinson SC . The plant cell wall-decomposing machinery underlies the functional diversity of forest fungi. *Science.* 2011;333:762–5.21764756
59. Ohm RA , Riley R , Salamov A , Min B , Choi I-G , Grigoriev IV . Genomics of wood-degrading fungi. *Fungal Genet Biol.* 2014 11;72:82–90.24853079
60. Nagy LG , Riley R , Tritt A , Adam C , Daum C , Floudas D , Sun H , Yadav JS , Pangilinan J , Larsson K-H , Matsuura K , Barry K , Labutti K , Kuo R , Ohm RA , Bhattacharya SS , Shirouzu T , Yoshinaga Y , Martin FM , Grigoriev IV , Hibbett DS . Comparative Genomics of Early-Diverging Mushroom-Forming Fungi Provides Insights into the Origins of Lignocellulose Decay Capabilities. *Mol Biol Evol.* 2016 4;33(4):959–70.26659563
61. Floudas D , Held BW , Riley R , Nagy LG , Koehler G , Ransdell AS , Younus H , Chow J , Chiniquy J , Lipzen A , Tritt A , Sun H , Haridas S , LaButti K , Ohm RA , Kües U , Blanchette RA , Grigoriev IV , Minto RE , Hibbett DS . Evolution of novel wood decay mechanisms in Agaricales revealed by the genome sequences of *Fistulina hepatica* and *Cylindrobasidium torrendii*. *Fungal Genet Biol.* 2015 3;76:78–92.25683379
62. Riley R , Salamov AA , Brown DW , Nagy LG , Floudas D , Held BW , Levasseur A , Lombard V , Morin E , Otillar R , Lindquist EA , Sun H , LaButti KM , Schmutz J , Jabbour D , Luo H , Baker SE , Pisabarro AG , Walton JD , Blanchette RA , Henrissat B , Martin F , Cullen D , Hibbett DS , Grigoriev IV . Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc Natl Acad Sci U S A.* 2014 7 8;111 (27):9923–8.24958869

63. Fernandez-Fueyo E , Ruiz-Dueñas FJ , Ferreira P , Floudas D , Hibbett DS , Canessa P , Larrondo LF , James TY , Seelenfreund D , Lobos S , Polanco R , Tello M , Honda Y , Watanabe T , Watanabe T , Ryu JS , Kubicek CP , Schmoll M , Gaskell J , Hammel KE , St. John FJ , Vanden Wymelenberg A , Sabat G , Splinter BonDurant S , Syed K , Yadav JS , Doddapaneni H , Subramanian V , Lavin JL , Oguiza JA , Perez G , Pisabarro AG , Ramirez L , Santoyo F , Master E , Coutinho PM , Henrissat B , Lombard V , Magnuson JK , Kües U , Hori C , Igarashi K , Samejima M , Held BW , Barry KW , LaButti KM , Lapidus A , Lindquist EA , Lucas SM , Riley R , Salamov AA , Hoffmeister D , Schwenk D , Hadar Y , Yarden O , de Vries RP , Wiebenga A , Stenlid J , Eastwood D , Grigoriev IV , Berka RM , Blanchette RA , Kersten P , Martinez AT , Vicuna R , Cullen D . Comparative genomics of Ceriporiopsis subvermispura and Phanerochaete chrysosporium provide insight into selective ligninolysis. *Proceedings of the National Academy of Sciences*. 2012 4 3;109(14):5458–63.
64. Orpin CG , Joblin KN . The rumen anaerobic fungi In: Hobson PN , Stewart CS , editors. *The Rumen Microbial Ecosystem*. Springer Netherlands; 1997 p. 140–95.
65. Orpin CG . Anaerobic fungi: taxonomy, biology and distribution in nature. *Anaerobic Fungi*. 1994;1–46.
66. Conley CA , Ishkhanova G , McKay CP , Cullings K . A preliminary survey of non-lichenized fungi cultured from the hyperarid Atacama Desert of Chile. *Astrobiology*. 2006 8;6(4):521–6.
67. Gonçalves VN , Cantrell CL , Wedge DE , Ferreira MC , Soares MA , Jacob MR , Oliveira FS , Galante D , Rodrigues F , Alves TMA , Zani CL , Junior PAS , Murta S , Romanha AJ , Barbosa EC , Kroon EG , Oliveira JG , Gomez-Silva B , Galetovic A , Rosa CA , Rosa LH . Fungi associated with rocks of the Atacama Desert: taxonomy, distribution, diversity, ecology and bioprospection for bioactive compounds. *Environ Microbiol*. 2016 1;18(1):232–45.26235221
68. Kogej T , Ramos J , Plemenitaš A , Gunde-Cimerman N . The Halophilic Fungus *Hortaea werneckii* and the Halotolerant Fungus *Aureobasidium pullulans* Maintain Low Intracellular Cation Concentrations in Hypersaline Environments. *Appl Environ Microbiol*. 2005 11 1;71(11):6600–5.16269687
69. Selbmann L , de Hoog GS , Mazzaglia A , Friedmann EI , Onofri S . Fungi at the edge of life: cryptendolithic black fungi from Antarctic desert. *Stud Mycol*. 2005;51:1–32.
70. Zucconi L , Onofri S , Cecchini C , Isola D , Ripa C , Fenice M , Madonna S , Reboleiro-Rivas P , Selbmann L . Mapping the lithic colonization at the boundaries of life in Northern Victoria Land, Antarctica. *Polar Biol*. 2016 1 1;39(1):91–102.
71. Powell AJ , Parchert KJ , Bustamante JM , Ricken JB , Hutchinson MI , Natvig DO . Thermophilic fungi in an aridland ecosystem. *Mycologia*. 2012 7 1;104(4):813–25.22505432
72. Morgenstern I , Powlowski J , Ishmael N , Darmond C , Marquateau S , Moisan M-C , Quenneville G , Tsang A . A molecular phylogeny of thermophilic fungi. *Fungal Biol*. 2012 4; 116(4):489–502.
73. Romanelli RA , Houston CW , Barnett SM . Studies on Thermophilic Cellulolytic Fungi. *Appl Microbiol*. 1975 8 1;30(2):276–81.
74. Berka RM , Grigoriev IV , Otillar R , Salamov A , Grimwood J , Reid I , Ishmael N , John T , Darmond C , Moisan M-C , Henrissat B , Coutinho PM , Lombard V , Natvig DO , Lindquist E , Schmutz J , Lucas S , Harris P , Powlowski J , Bellemare A , Taylor D , Butler G , de Vries RP , Allijn IE , van den Brink J , Ushinsky S , Storms R , Powell AJ , Paulsen IT , Elbourne LDH , Baker SE , Magnuson J , LaBoissiere S , John Clutterbuck A , Martinez D , Wogulis M , de Leon AL , Rey MW , Tsang A . Comparative genomic analysis of the thermophilic biomassdegrading fungi *Myceliophthora thermophila* and *Thielavia terrestris*. *Nat Biotechnol*. 2011 10 2;29(10):922–7.21964414
75. Amlacher S , Sarges P , Flemming D , van Noort V , Kunze R , Devos DP , Arumugam M , Bork P , Hurt E . Insight into Structure and Assembly of the Nuclear Pore Complex by Utilizing the Genome of a Eukaryotic Thermophile. *Cell*. 2011 7 22;146(2):277–89.21784248
76. Keeling PJ , Slamovits CH . Simplicity and complexity of microsporidian genomes. *Eukaryot Cell*. 2004 12;3(6):1363–9.15590811
77. Akiyoshi DE , Morrison HG , Lei S , Feng X , Zhang Q , Corradi N , Mayanja H , Tumwine JK , Keeling PJ , Weiss LM , Tzipori S . Genomic survey of the non-cultivable opportunistic human pathogen, *Enterocytozoon bieneusi*. *PLoS Pathog*. 2009 Jan;5(1):e1000261.19132089

78. Corradi N, Haag KL, Pombert J-F, Ebert D, Keeling PJ. Draft genome sequence of the *Daphnia* pathogen *Octospora bayeri*: insights into the gene content of a large microsporidian genome and a model for host-parasite interactions. *Genome Biol.* 2009 10 6;10(10):R106.19807911
79. Pombert J-F, Xu J, Smith DR, Heiman D, Young S, Cuomo CA, Weiss LM, Keeling PJ. Complete genome sequences from three genetically distinct strains reveal high intraspecies genetic diversity in the microsporidian *Encephalitozoon cuniculi*. *Eukaryot Cell.* 2013 4;12(4):503–11.23291622
80. Goffeau A, Barrell BG, Bussey H, Davis RW, Dujon B, Feldmann H, Galibert F, Hoheisel JD, Jacq C, Johnston M, Louis EJ, Mewes HW, Murakami Y, Philippsen P, Tettelin H, Oliver SG. Life with 6000 genes. *Science.* 1996 10 25;274(5287):546, 563–7.8849441
81. Wood V, Gwilliam R, Rajandream M-A, Lyne M, Lyne R, Stewart A, Sgouros J, Peat N, Hayles J, Baker S, Basham D, Bowman S, Brooks K, Brown D, Brown S, Chillingworth T, Churcher C, Collins M, Connor R, Cronin A, Davis P, Feltwell T, Fraser A, Gentles S, Goble A, Hamlin N, Harris D, Hidalgo J, Hodgson G, Holroyd S, Hornsby T, Howarth S, Huckle EJ, Hunt S, Jagels K, James K, Jones L, Jones M, Leather S, McDonald S, McLean J, Mooney P, Moule S, Mungall K, Murphy L, Niblett D, Odell C, Oliver K, O’Neil S, Pearson D, Quail MA, Rabinowitsch E, Rutherford K, Rutter S, Saunders D, Seeger K, Sharp S, Skelton J, Simmonds M, Squares R, Squares S, Stevens K, Taylor K, Taylor RG, Tivey A, Walsh S, Warren T, Whitehead S, Woodward J, Volckaert G, Aert R, Robben J, Grymonprez B, Weltjens I, Vanstreels E, Rieger M, Schäfer M, Müller-Auer S, Gabel C, Fuchs M, Fritz C, Holzer E, Moestl D, Hilbert H, Borzym K, Langer I, Beck A, Lehrach H, Reinhardt R, Pohl TM, Eger P, Zimmermann W, Wedler H, Wambutt R, Purnelle B, Goffeau A, Cadieu E, Dreano S, Gloux S, Lelaure V, Mottier S, Galibert F, Aves SJ, Xiang Z, Hunt C, Moore K, Hurst SM, Lucas M, Rochet M, Gaillardin C, Tallada VA, Garzon A, Thode G, Daga RR, Cruzado L, Jimenez J, Sánchez M, del Rey F, Benito J, Domínguez A, Revuelta JL, Moreno S, Armstrong J, Forsburg SL, Cerrutti L, Lowe T, McCombie WR, Paulsen I, Potashkin J, Shpakovski GV, Ussery D, Barrell BG, Nurse P. The genome sequence of *Schizosaccharomyces pombe*. *Nature.* 2002 2 21;415(6874):871–80.11859360
82. James TY, Pelin A, Bonen L, Ahrendt S, Sain D, Corradi N, Stajich JE. Shared Signatures of Parasitism and Phylogenomics Unite Cryptomycota and Microsporidia. *Curr Biol.* 2013;23(16):1548–53.23932404
83. Toome M, Ohm RA, Riley RW, James TY, Lazarus KL, Henrissat B, Albu S, Boyd A, Chow J, Clum A, Heller G, Lipzen A, Nolan M, Sandor L, Zvenigorodsky N, Grigoriev IV, Spatafora JW, Aime MC. Genome sequencing provides insight into the reproductive biology, nutritional mode and ploidy of the fern pathogen *Mixia osmundae*. *New Phytol.* 2014 4;202(2):554–64.24372469
84. Janbon G, Ormerod KL, Paulet D, Byrnes EJ, Yadav V, Chatterjee G, Mullapudi N, Hon C-C, Billmyre RB, Brunel F, Bahn Y-S, Chen W, Chen Y, Chow EWL, Coppée J-Y, Floyd-Averette A, Gaillardin C, Gerik KJ, Goldberg J, Gonzalez-Hilarion S, Gujja S, Hamlin JL, Hsueh Y-P, Ianiri G, Jones S, Kodira CD, Kozubowski L, Lam W, Marra M, Mesner LD, Mieczkowski PA, Moyrand F, Nielsen K, Proux C, Rossignol T, Schein JE, Sun S, Wollschlaeger C, Wood IA, Zeng Q, Neuveglise C, Newlon CS, Perfect JR, Lodge JK, Idnurm A, Stajich JE, Kronstad JW, Sanyal K, Heitman J, Fraser JA, Cuomo CA, Dietrich FS. Analysis of the Genome and Transcriptome of *Cryptococcus neoformans* var. *grubii* Reveals Complex RNA Expression and Microevolution Leading to Virulence Attenuation. *PLoS Genet.* 2014 4 17;10(4):e1004261.24743168
85. Loftus BJ, Fung E, Roncaglia P, Rowley D, Amedeo P, Bruno D, Vamathevan J, Miranda M, Anderson IJ, Fraser JA, Allen JE, Bosdet IE, Brent MR, Chiu R, Doering TL, Donlin MJ, D’Souza CA, Fox DS, Grinberg V, Fu J, Fukushima M, Haas BJ, Huang JC, Janbon G, Jones SJM, Koo HL, Krzywinski MI, Kwon-Chung JK, Lengeler KB, Maiti R, Marra MA, Marra RE, Mathewson CA, Mitchell TG, Perteu M, Riggs FR, Salzberg SL, Schein JE, Shvartsbeyn A, Shin H, Shumway M, Specht CA, Suh BB, Tenney A, Utterback TR, Wickes BL, Wortman JR, Wye NH, Kronstad JW, Lodge JK, Heitman J, Davis RW, Fraser CM, Hyman RW. The genome of the basidiomycetous yeast and human pathogen *Cryptococcus neoformans*. *Science.* 2005 2 25;307(5713):1321–4.15653466

86. D'Souza CA , Kronstad JW , Taylor G , Warren R , Yuen M , Hu G , Jung WH , Sham A , Kidd SE , Tangen K , Lee N , Zeilmaker T , Sawkins J , McVicker G , Shah S , Gnerre S , Griggs A , Zeng Q , Bartlett K , Li W , Wang X , Heitman J , Stajich JE , Fraser JA , Meyer W , Carter D , Schein J , Krzywinski M , Kwon-Chung KJ , Varma A , Wang J , Brunham R , Fyfe M , Ouellette BFF , Siddiqui A , Marra M , Jones S , Holt R , Birren BW , Galagan JE , Cuomo CA . Genome variation in *Cryptococcus gattii*, an emerging pathogen of immunocompetent hosts. *MBio*. 2011 28;2(1):e00342–10.21304167
87. Dujon B , Sherman D , Fischer G , Durrens P , Casaregola S , Lafontaine I , De Montigny J , Marck C , Neuveglise C , Talla E , Goffard N , Frangeul L , Aigle M , Anthouard V , Babour A , Barbe V , Barnay S , Blanchin S , Beckerich J-M , Beyne E , Bleykasten C , Boisramé A , Boyer J , Cattolico L , Confanioleri F , De Daruvar A , Despons L , Fabre E , Fairhead C , Ferry-Dumazet H , Groppi A , Hantraye F , Hennequin C , Jauniaux N , Joyet P , Kachouri R , Kerrest A , Koszul R , Lemaire M , Lesur I , Ma L , Muller H , Nicaud J-M , Nikolski M , Oztas S , Ozier-Kalogeropoulos O , Pellenz S , Potier S , Richard G-F , Straub M-L , Suleau A , Swennen D , Tekaiia F , Wesolowski-Louvel M , Westhof E , Wirth B , Zeniou-Meyer M , Zivanovic I , Bolotin-Fukuhara M , Thierry A , Bouchier C , Caudron B , Scarpelli C , Gaillardin C , Weissenbach J , Wincker P , Souciet J-L . Genome evolution in yeasts. *Nature*. 2004 7 1;430(6995):35–44.15229592
88. Peter M , Kohler A , Ohm RA , Kuo A , Krützmann J , Morin E , Arend M , Barry KW , Binder M , Choi C , Clum A , Copeland A , Grisel N , Haridas S , Kipfer T , LaButti K , Lindquist E , Lipzen A , Maire R , Meier B , Mihaltcheva S , Molinier V , Murat C , Pöggeler S , Alisha Quandt C , Sperisen C , Tritt A , Tisserant E , Crous PW , Henrissat B , Nehls U , Egli S , Spatafora JW , Grigoriev IV , Martin FM . Ectomycorrhizal ecology is imprinted in the genome of the dominant symbiotic fungus *Cenococcum geophilum*. *Nat Commun*. 2016 9 7;7:12662.27601008
89. Martin F , Kohler A , Murat C , Balestrini R , Coutinho PM , Jaillon O , Montanini B , Morin E , Noel B , Percudani R , Porcel B , Rubini A , Amicucci A , Amselem J , Anthouard V , Arcioni S , Artiguenave F , Aury J-M , Ballario P , Bolchi A , Brenna A , Brun A , Buée M , Cantarel B , Chevalier G , Couloux A , Da Silva C , Denoeud F , Duplessis S , Ghignone S , Hilselberger B , Iotti M , Marçais B , Mello A , Miranda M , Pacioni G , Quesneville H , Riccioni C , Ruotolo R , Splivallo R , Stocchi V , Tisserant E , Viscomi AR , Zambonelli A , Zampieri E , Henrissat B , Lebrun M-H , Paolocci F , Bonfante P , Ottonello S , Wincker P . Périgord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. *Nature*. 2010 3 28;464(7291):1033–8.20348908
90. Spanu PD , Abbott JC , Amselem J , Burgis TA , Soanes DM , Stüber K , Loren van Themaat EV , Brown JKM , Butcher SA , Gurr SJ , Lebrun M-H , Ridout CJ , Schulze-Lefert P , Talbot NJ , Ahmadinejad N , Ametz C , Barton GR , Benjdia M , Bidzinski P , Bindschedler LV , Both M , Brewer MT , Cadle-Davidson L , Cadle-Davidson MM , Collemare J , Cramer R , Frenkel O , Godfrey D , Harriman J , Hoede C , King BC , Klages S , Kleemann J , Knoll D , Koti PS , Kreplak J , López-Ruiz FJ , Lu X , Maekawa T , Mahanil S , Micali C , Milgroom MG , Montana G , Noir S , O'Connell RJ , Oberhaensli S , Parlange F , Pedersen C , Quesneville H , Reinhardt R , Rott M , Sacristán S , Schmidt SM , Schön M , Skamnioti P , Sommer H , Stephens A , Takahara H , Thordal-Christensen H , Vigouroux M , Weßling R , Wicker T , Panstruga R . Genome Expansion and Gene Loss in Powdery Mildew Fungi Reveal Tradeoffs in Extreme Parasitism. *Science*. 2010 12;330(6010):1543–6.21148392
91. Murrin F , Holtby J , Noland RA , Davidson WS . The genome of *Entomophaga aulicae* (Entomophthorales, Zygomycetes): Base composition and size. *Exp Mycol*. 1986 3 1;10(1):67–75.
92. De Fine Licht HH , Jensen AB , Eilenberg J . Comparative transcriptomics reveal host-specific nucleotide variation in entomophthoralean fungi. *Mol Ecol*. 2017 4;26(7):2092–110.27717247
93. Małagocka J , Grell MN , Lange L , Eilenberg J , Jensen AB . Transcriptome of an entomophthoralean fungus (*Pandora formicae*) shows molecular machinery adjusted for successful host exploitation and transmission. *J Invertebr Pathol*. 2015 6;128:47–56.25968105
94. Tavares S , Ramos AP , Pires AS , Azinheira HG , Caldeirinha P , Link T , Abranches R , Silva M do C , Voegelé RT , Loureiro J , Talhinhos P . Genome size analyses of Pucciniales reveal the largest fungal genomes. *Front Plant Sci*. 2014;5:422.25206357

95. Williams BAP , Lee RCH , Becnel JJ , Weiss LM , Fast NM , Keeling PJ . Genome sequence surveys of *Brachiola algerae* and *Edhazardia aedis* reveal microsporidia with low gene densities. *BMC Genomics*. 2008 4 29;9:200.18445287
96. Katinka MD , Duprat S , Cornillot E , Méténier G , Thomarat F , Prensier G , Barbe V , Peyretailade E , Brottier P , Wincker P , Delbac F , El Alaoui H , Peyret P , Saurin W , Gouy M , Weissenbach J , Vivares CP . Genome sequence and gene compaction of the eukaryote parasite *Encephalitozoon cuniculi*. *Nature*. 2001 11 22;414(6862):450–3.11719806
97. Cuomo CA , Desjardins CA , Bakowski MA , Goldberg J , Ma AT , Becnel JJ , Didier ES , Fan L , Heiman DI , Levin JZ , Young S , Zeng Q , Troemel ER . Microsporidian genome analysis reveals evolutionary strategies for obligate intracellular growth. *Genome Res*. 2012 12;22(12):2478–88.22813931
98. Troemel ER , Becnel JJ . Genome analysis and polar tube firing dynamics of mosquito-infecting microsporidia. *Fungal Genet Biol*. 2015 10;83:41–4.26300319
99. Corradi N , Akiyoshi DE , Morrison HG , Feng X , Weiss LM , Tzipori S , Keeling PJ . Patterns of genome evolution among the microsporidian parasites *Encephalitozoon cuniculi*, *Antonospora locustae* and *Enterocytozoon bieneusi*. *PLoS One*. 2007 12 5;2(12):e1277.18060071
100. Corradi N , Gangaeva A , Keeling PJ . Comparative profiling of overlapping transcription in the compacted genomes of microsporidia *Antonospora locustae* and *Encephalitozoon cuniculi*. *Genomics*. 2008 4;91(4):388–93.18280697
101. Hauser PM , Burdet FX , Cissé OH , Keller L , Taffé P , Sanglard D , Pagni M . Comparative genomics suggests that the fungal pathogen *pneumocystis* is an obligate parasite scavenging amino acids from its host's lungs. Stajich JE , editor. *PLoS One*. 2010 12 20;5(12):e15152.21188143
102. Cissé OH , Pagni M , Hauser PM . De novo assembly of the *Pneumocystis jirovecii* genome from a single bronchoalveolar lavage fluid specimen from a patient. *MBio*. 2012 12 26;4(1):e00428–12.23269827
103. Almeida JMGC , Cissé OH , Fonseca Á , Pagni M , Hauser PM . Comparative genomics suggests primary homothallism of *Pneumocystis* species. *MBio*. 2015 1 13;6(1):e02250–14.25587012
104. Dietrich FS , Voegeli S , Brachat S , Lerch A , Gates K , Steiner S , Mohr C , Pöhlmann R , Luedi P , Choi S , Wing RA , Flavier A , Gaffney TD , Philippsen P . The *Ashbya gossypii* Genome as a Tool for Mapping the Ancient *Saccharomyces cerevisiae* Genome. *Science*. 2004 4 9;304(5668):304–7.15001715
105. Raffaele S , Kamoun S . Genome evolution in filamentous plant pathogens: why bigger can be better. *Nat Rev Microbiol*. 2012 5 8;10(6):417–30.22565130
106. Dong S , Raffaele S , Kamoun S . The two-speed genomes of filamentous pathogens: waltz with plants. *Curr Opin Genet Dev*. 2015 12;35:57–65.26451981
107. Rouxel T , Grandaubert J , Hane JK , Hoede C , van de Wouw AP , Couloux A , Dominguez V , Anthouard V , Bally P , Bourras S , Cozijnsen AJ , Ciuffetti LM , Degraeve A , Dilmaghani A , Duret L , Fudal I , Goodwin SB , Gout L , Glaser N , Linglin J , Kema GH , Lapalu N , Lawrence CB , May K , Meyer M , Ollivier B , Poulain J , Schoch CL , Simon A , Spatafora JW , Stachowiak A , Turgeon BG , Tyler BM , Vincent D , Weissenbach J , Amselem J , Quesneville H , Oliver RP , Wincker P , Balesdent MH , Howlett BJ . Effector diversification within compartments of the *Leptosphaeria maculans* genome affected by Repeat-Induced Point mutations. *Nat Commun*. 2011;2:202.21326234
108. Raffaele S , Farrer RA , Cano LM , Studholme DJ , MacLean D , Thines M , Jiang RHY , Zody MC , Kunjeti SG , Donofrio NM , Meyers BC , Nusbaum C , Kamoun S . Genome evolution following host jumps in the Irish potato famine pathogen lineage. *Science*. 2010 12 10;330(6010):1540–3.21148391
109. Sperschneider J , Gardiner DM , Thatcher LF , Lyons R , Singh KB , Manners JM , Taylor JM . Genome-Wide Analysis in Three *Fusarium* Pathogens Identifies Rapidly Evolving Chromosomes and Genes Associated with Pathogenicity. *Genome Biol Evol*. 2015 5 19;7(6):1613–27.25994930
110. Croll D , McDonald BA . The accessory genome as a cradle for adaptive evolution in pathogens. *PLoS Pathog*. 2012 4 26;8(4):e1002608.22570606

111. Grandaubert J , Lowe R , Soyer J , Schoch C , Van de Wouw A , Fudal I , Robbertse B , Lapalu N , Links M , Ollivier B , Linglin J , Barbe V , Mangenot S , Cruaud C , Borhan H , Howlett B , Balesdent M-H , Rouxel T . Transposable element-assisted evolution and adaptation to host plant within the *Leptosphaeria maculans*-*Leptosphaeria biglobosa* species complex of fungal pathogens. *BMC Genomics*. 2014;15(1):891.25306241
112. Faino L , Seidl MF , Shi-Kunne X , Pauper M , van den Berg GCM , Wittenberg AHJ , Thomma BPHJ. Transposons passively and actively contribute to evolution of the two-speed genome of a fungal pathogen. *Genome Res*. 2016 8;26(8):1091–100.27325116
113. Burke DT , Carle GF , Olson MV . Cloning of large segments of exogenous DNA into yeast by means of artificial chromosome vectors. *Science*. 1987 5 15;236(4803):806–12.3033825
114. Galitski T , Saldanha AJ , Styles CA , Lander ES , Fink GR . Ploidy regulation of gene expression. *Science*. 1999 7 9;285(5425):251–4.10398601
115. Mable BK , Otto SP . Masking and purging mutations following EMS treatment in haploid, diploid and tetraploid yeast (*Saccharomyces cerevisiae*). *Genet Res*. 2001 2;77(1):9–26.11279834
116. Torres EM , Sokolsky T , Tucker CM , Chan LY , Boselli M , Dunham MJ , Amon A . Effects of aneuploidy on cellular physiology and cell division in haploid yeast. *Science*. 2007 8 17;317(5840):916–24.17702937
117. Lynch M , Conery JS . The origins of genome complexity. *Science*. 2003;302:1401–4.14631042
118. Lynch M The origins of genome architecture Sunderland, MA: Sinauer Associates; 2007.
119. Huerta-Cepas J , Capella-Gutiérrez S , Pryszcz LP , Marcet-Houben M , Gabaldón T. PhylomeDB v4: zooming into the plurality of evolutionary histories of a genome. *Nucleic Acids Res*. 2014 1;42(Database issue):D897–902.24275491
120. Kersey PJ , Allen JE , Christensen M , Davis P , Falin LJ , Grabmueller C , Hughes DST , Humphrey J , Kerhornou A , Khobova J , Langridge N , McDowall MD , Maheswari U , Maslen G , Nuhn M , Ong CK , Paulini M , Pedro H , Toneva I , Tuli MA , Walts B , Williams G , Wilson D , Youens-Clark K , Monaco MK , Stein J , Wei X , Ware D , Bolser DM , Howe KL , Kulesha E , Lawson D , Staines DM . Ensembl Genomes 2013: scaling up access to genome-wide data. *Nucleic Acids Res*. 2014 1;42(Database issue):D546–52.24163254
121. Akcapinar GB , Kappel L , Sezerman OU , Seidl-Seiboth V . Molecular diversity of LysM carbohydrate-binding motifs in fungi. *Curr Genet*. 2015 5;61(2):103–13.25589417
122. Kombrink A , Thomma BPHJ . LysM effectors: secreted proteins supporting fungal life. *PLoS Pathog*. 2013 12 12;9(12):e1003769.24348247
123. Teixeira MM , de Almeida LGP , Kubitschek-Barreira P , Alves FL , Kioshima ES , Abadio AKR , Fernandes L , Derengowski LS , Ferreira KS , Souza RC , Ruiz JC , de Andrade NC , Paes HC , Nicola AM , Albuquerque P , Gerber AL , Martins VP , Peconick LDF , Neto AV , Chaucanez CB , Silva PA , Cunha OL , de Oliveira FFM , dos Santos TC , Barros ALN , Soares MA , de Oliveira LM , Marini MM , Villalobos-Duno H , Cunha MML , de Hoog S , da Silveira JF , Henrissat B , Nino-Vega GA , Cisalpino PS , Mora-Montes HM , Almeida SR , Stajich JE , Lopes-Bezerra LM , Vasconcelos ATR , Felipe MSS . Comparative genomics of the major fungal agents of human and animal Sporotrichosis: *Sporothrix schenckii* and *Sporothrix brasiliensis*. *BMC Genomics*. 2014 10 29;15(1):943.25351875
124. Martinez DA , Oliver BG , Gräser Y , Goldberg JM , Li W , Martinez-Rossi NM , Monod M , Shelest E , Barton RC , Birch E , Brakhage AA , Chen Z , Gurr SJ , Heiman D , Heitman J , Kosti I , Rossi A , Saif S , Samalova M , Saunders CW , Shea T , Summerbell RC , Xu J , Young S , Zeng Q , Birren BW , Cuomo CA , White TC . Comparative genome analysis of *Trichophyton rubrum* and related dermatophytes reveals candidate genes involved in infection. *MBio*. 2012 9 4;3(5):e00259–12.22951933
125. Buist G , Steen A , Kok J , Kuipers OP . LysM, a widely distributed protein motif for binding to (peptido)glycans. *Mol Microbiol*. 2008 5 1;68(4):838–47.18430080
126. de Jonge R , van Esse HP , Kombrink A , Shinya T , Desaki Y , Bours R , van der Krol S , Shibuya N , Matthieu HA , Bart P H . Conserved Fungal LysM Effector Ecp6 Prevents Chitin-Triggered Immunity in Plants. *Science*. 2010 8 20;329(5994):953–5.20724636

127. Xue C , Liu T , Chen L , Li W , Liu I , Kronstad JW , Seyfang A , Heitman J . Role of an expanded inositol transporter repertoire in *Cryptococcus neoformans* sexual reproduction and virulence. *MBio*. 2010 5 18;1(1):e00084–10.20689743
128. Zaragoza O , Rodrigues ML , De Jesus M , Frases S , Dadachova E , Casadevall A . Chapter 4 The Capsule of the Fungal Pathogen *Cryptococcus neoformans*. In: *Advances in Applied Microbiology*. Academic Press; 2009 p. 133–216.
129. Perfect JR . *Cryptococcus neoformans*: a sugar-coated killer with designer genes. *FEMS Immunol Med Microbiol*. 2005 9 1;45(3):395–404.16055314
130. O'Meara TR , Alspaugh JA . The *Cryptococcus neoformans* capsule: a sword and a shield. *Clin Microbiol Rev*. 2012 7;25(3):387–408.22763631
131. Li J , Zhang K-Q . Independent expansion of zincin metalloproteinases in *Onygenales* fungi may be associated with their pathogenicity. *PLoS One*. 2014 2 28;9(2):e90225.24587291
132. Whiston E , Taylor JW . Genomics in *Coccidioides*: insights into evolution, ecology, and pathogenesis. *Med Mycol*. 2014 2;52(2):149–55.24576996
133. Muñoz JF , Gauthier GM , Desjardins CA , Gallo JE , Holder J , Sullivan TD , Marty AJ , Carmen JC , Chen Z , Ding L , Gujja S , Magrini V , Misas E , Mitreva M , Priest M , Saif S , Whiston EA , Young S , Zeng Q , Goldman WE , Mardis ER , Taylor JW , McEwen JG , Clay OK , Klein BS , Cuomo CA . The Dynamic Genome and Transcriptome of the Human Fungal Pathogen *Blastomyces* and Close Relative *Emmonsia*. *PLoS Genet*. 2015 10 6;11(10):e1005493.26439490
134. Joneson S , Stajich JE , Shiu S-H , Rosenblum EB . Genomic transition to pathogenicity in chytrid fungi. *PLoS Pathog*. 2011 11 3;7(11):e1002338.22072962
135. Thekkiniath JC , Zabet-Moghaddam M , San Francisco SK , San Francisco MJ . A novel subtilisin-like serine protease of *Batrachochytrium dendrobatidis* is induced by thyroid hormone and degrades antimicrobial peptides. *Fungal Biol*. 2013 6;117(6):451–61.23809655
136. Abramyan J , Stajich JE . Species-specific chitin-binding module 18 expansion in the amphibian pathogen *Batrachochytrium dendrobatidis*. *MBio*. 2012;3:e00150–12.22718849
137. Farrer RA , Martel A , Verbrugghe E , Abouelleil A , Ducatelle R , Longcore JE , James TY , Pasmans F , Fisher MC , Cuomo CA . Genomic innovations linked to infection strategies across emerging pathogenic chytrid fungi. *Nat Commun*. 2017 3 21;8:14742.28322291
138. Liu P , Stajich JE . Characterization of the Carbohydrate Binding Module 18 gene family in the amphibian pathogen *Batrachochytrium dendrobatidis*. *Fungal Genet Biol*. 2015 4;77:31–9.25819009
139. Pendleton AL , Smith KE , Feau N , Martin FM , Grigoriev IV , Hamelin R , Nelson CD , Burleigh JG , Davis JM . Duplications and losses in gene families of rust pathogens highlight putative effectors. *Front Plant Sci*. 2014;5:299.25018762
140. Goodwin SB , Ben M'Barek S , Dhillon B , Wittenberg AHJ , Crane CF , Hane JK , Foster AJ , Van der Lee TAJ , Grimwood J , Aerts A , Antoniw J , Bailey A , Bluhm B , Bowler J , Bristow J , van der Burgt A , Canto-Canché B , Churchill ACL , Conde-Ferràez L , Cools HJ , Coutinho PM , Csukai M , Dehal P , De Wit P , Donzelli B , van de Geest HC , van Ham RCHJ , Hammond-Kosack KE , Henrissat B , Kilian A , Kobayashi AK , Koopmann E , Kourmpetis Y , Kuzniar A , Lindquist E , Lombard V , Maliepaard C , Martins N , Mehrabi R , Nap JPH , Ponomarenko A , Rudd JJ , Salamov A , Schmutz J , Schouten HJ , Shapiro H , Stergiopoulos I , Torriani SFF , Tu H , de Vries RP , Waalwijk C , Ware SB , Wiebenga A , Zwiers L-H , Oliver RP , Grigoriev IV , Kema GHJ . Finished Genome of the Fungal Wheat Pathogen *Mycosphaerella graminicola* Reveals Dispensome Structure, Chromosome Plasticity, and Stealth Pathogenesis. *PLoS Genet*. 2011 6 9;7(6):e1002070.21695235
141. Hu X , Xiao G , Zheng P , Shang Y , Su Y , Zhang X , Liu X , Zhan S , St. Leger RJ , Wang C . Trajectory and genomic determinants of fungal-pathogen speciation and host adaptation. *Proceedings of the National Academy of Sciences*. 2014 11 25;111 (47): 16796–801.
142. Gao Q , Jin K , Ying S-H , Zhang Y , Xiao G , Shang Y , Duan Z , Hu X , Xie X-Q , Zhou G , Peng G , Luo Z , Huang W , Wang B , Fang W , Wang S , Zhong Y , Ma L-J , St Leger RJ , Zhao G-P , Pei Y , Feng M-G , Xia Y , Wang C . Genome sequencing and comparative transcriptomics of the model entomopathogenic fungi *Metarhizium anisopliae* and *M. acridum*. *PLoS Genet* 2011 1 6;7(1):e1001264.21253567

143. Schiøtt M , De Fine Licht HH , Lange L , Boomsma JJ . Towards a molecular understanding of symbiont function: Identification of a fungal gene for the degradation of xylan in the fungus gardens of leaf-cutting ants. *BMC Microbiol.* 2008;8(1):40.18307762
144. De Fine Licht HH , Schiøtt M , Mueller UG , Boomsma JJ . Evolutionary transitions in enzyme activity of ant fungus gardens. *Evolution.* 2010 7;64(7):2055–69.20067517
145. Nygaard S , Zhang G , Schiøtt M , Li C , Wurm Y , Hu H , Zhou J , Ji L , Qiu F , Rasmussen M , Pan H , Hauser F , Krogh A , Grimmelikhuijzen CJP , Wang J , Boomsma JJ . The genome of the leaf-cutting ant *Acromyrmex echinator* suggests key adaptations to advanced social life and fungus farming. *Genome Res.* 2011 8 1;21(8):1339–48.21719571
146. De Fine Licht HH , Schiøtt M , Rogowska-Wrzesinska A , Nygaard S , Roepstorff P , Boomsma JJ . Laccase detoxification mediates the nutritional alliance between leaf-cutting ants and fungus-garden symbionts. *Proc Natl Acad Sci U S A.* 2013 1 8; 110(2):583–7.23267060
147. De Fine Licht HH , Boomsma JJ , Tunlid A . Symbiotic adaptations in the fungal cultivar of leaf-cutting ants. *Nat Commun.* 2014 12 1;5:5675.25435021
148. Aylward FO , Khadempour L , Tremmel DM , McDonald BR , Nicora CD , Wu S , Moore RJ , Orton DJ , Monroe ME , Piehowski PD , Purvine SO , Smith RD , Lipton MS , Burnum-Johnson KE , Currie CR . Enrichment and Broad Representation of Plant Biomass-Degrading Enzymes in the Specialized Hyphal Swellings of *Leucoagaricus gongylophorus*, the Fungal Symbiont of Leaf-Cutter Ants. *Brady S, editor. PLoS One.* 2015 8 28;10(8):e0134752.26317212
149. Khadempour L , Burnum-Johnson KE , Baker ES , Nicora CD , Webb-Robertson B-JM , White RA , Monroe ME , Huang EL , Smith RD , Currie CR . The fungal cultivar of leaf-cutter ants produces specific enzymes in response to different plant substrates. *Mol Ecol.* 2016 11 1 ;25(22): 5795–805.27696597
150. Corrochano LM , Kuo A , Marcet-Houben M , Polaino S , Salamov A , Villalobos-Escobedo JM , Grimwood J , Álvarez MI , Avalos J , Bauer D , Benito EP , Benoit I , Burger G , Camino LP , Canovas D , Cerdá-Olmedo E , Cheng J-F , Domínguez A , Eliáš M , Eslava AP , Glaser F , Gutiérrez G , Heitman J , Henrissat B , Iturriaga EA , Lang BF , Lavín JL , Lee SC , Li W , Lindquist E , López-García S , Luque EM , Marcos AT , Martin J , McCluskey K , Medina HR , Miralles-Durán A , Miyazaki A , Muñoz-Torres E , Oguiza JA , Ohm RA , Olmedo M , Orejas M , Ortiz-Castellanos L , Pisabarro AG , Rodríguez-Romero J , Ruiz-Herrera J , Ruiz-Vázquez R , Sanz C , Schackwitz W , Shahriari M , Shelest E , Silva-Franco F , Soanes D , Syed K , Tagua VG , Talbot NJ , Thon MR , Tice H , de Vries RP , Wiebenga A , Yadav JS , Braun EL , Baker SE , Garre V , Schmutz J , Horwitz BA , Torres-Martinez S , Idnurm A , Herrera-Estrella A , Gabaldón T , Grigoriev IV . Expansion of Signal Transduction Pathways in Fungi by Extensive Genome Duplication. *Curr Biol.* 2016 6 20;26(12):1577–84.27238284
151. Ma LJ , Ibrahim AS , Skory C , Grabherr MG , Burger G , Butler M , Elias M , Idnurm A , Lang BF , Sone T , Abe A , Calvo SE , Corrochano LM , Engels R , Fu J , Hansberg W , Kim JM , Kodira CD , Koehrsen MJ , Liu B , Miranda-Saavedra D , O’Leary S , Ortiz-Castellanos L , Poulter R , Rodríguez-Romero J , Ruiz-Herrera J , Shen YQ , Zeng Q , Galagan J , Birren BW , Cuomo CA , Wickes BL . Genomic analysis of the basal lineage fungus *Rhizopus oryzae* reveals a whole-genome duplication. *PLoS Genet.* 2009;5:e1000549.19578406
152. Stajich JE , Wilke SK , Ahren D , Au CH , Birren BW , Borodovsky M , Burns C , Canbäck B , Casselton LA , Cheng CK , Deng J , Dietrich FS , Fargo DC , Farman ML , Gathman AC , Goldberg J , Guigó R , Hoegger PJ , Hooker JB , Huggins A , James TY , Kamada T , Kilaru S , Kodira C , Kües U , Kupfer D , Kwan HS , Lomsadze A , Li W , Lilly WW , Ma L-J , Mackey AJ , Manning G , Martin F , Muraguchi H , Natvig DO , Palmerini H , Ramesh MA , Rehmeier CJ , Roe BA , Shenoy N , Stanke M , Ter-Hovhannisyan V , Tunlid A , Velagapudi R , Vision TJ , Zeng Q , Zolan ME , Pukkila PJ . Insights into evolution of multicellular fungi from the assembled chromosomes of the mushroom *Coprinopsis cinerea* (*Coprinus cinereus*). *Proc Natl Acad Sci U S A.* 2010 6 29;107(26):11889–94.20547848
153. Plett JM , Gibon J , Kohler A , Duffy K , Hoegger PJ , Velagapudi R , Han J , Kues U , Grigoriev IV , Martin F . Phylogenetic, genomic organization and expression analysis of hydrophobin genes in the ectomycorrhizal basidiomycete *Laccaria bicolor*. *Fungal Genet Biol.* 2012;49:199–209.22293303

154. Rineau F, Lmalem H, Ahren D, Shah F, Johansson T, Coninx L, Ruytinx J, Nguyen H, Grigoriev I, Kuo A, Kohler A, Morin E, Vangronsveld J, Martin F, Colpaert JV. Comparative genomics and expression levels of hydrophobins from eight mycorrhizal genomes. *Mycorrhiza*. 2017 19;1–14.
155. Sammer D, Krause K, Gube M, Wagner K, Kothe E. Hydrophobins in the Life Cycle of the Ectomycorrhizal Basidiomycete *Tricholoma vaccinum*. *PLoS One*. 2016 12 9;11(12):e0167773.27936063
156. Martinez D, Larrondo LF, Putnam N, Sollewijn Gelpke MD, Huang K, Chapman J, Helfenbein KG, Ramaiya P, Chris Detter J, Larimer F, Coutinho PM, Henrissat B, Berka R, Cullen D, Rokhsar D. Genome sequence of the lignocellulose degrading fungus *Phanerochaete chrysosporium* strain RP78. *Nat Biotechnol*. 2004 5 2;22(6):695–700.15122302
157. Doddapaneni H, Chakraborty R, Yadav JS. Genome-wide structural and evolutionary analysis of the P450 monooxygenase genes (P450ome) in the white rot fungus *Phanerochaete chrysosporium*: evidence for gene duplications and extensive gene clustering. *BMC Genomics*. 2005;6(1):92.15955240
158. Yadav JS, Doddapaneni H, Subramanian V. P450ome of the white rot fungus *Phanerochaete chrysosporium*: structure, evolution and regulation of expression of genomic P450 clusters. *Biochem Soc Trans*. 2006 12;34(Pt 6): 1165–9.17073777
159. Syed K, Yadav JS. P450 monooxygenases (P450ome) of the model white rot fungus *Phanerochaete chrysosporium*. *Crit Rev Microbiol*. 2012 11;38(4):339–63.22624627
160. Syed K, Nelson DR, Riley R, Yadav JS. Genomewide annotation and comparative genomics of cytochrome P450 monooxygenases (P450s) in the polypore species *Bjerkandera adusta*, *Ganoderma* sp. and *Phlebia brevispora*. *Mycologia*. 2013;105(6):1445–55.23928414
161. Syed K, Shale K, Pagadala NS, Tuszyński J. Systematic Identification and Evolutionary Analysis of Catalytically Versatile Cytochrome P450 Monooxygenase Families Enriched in Model Basidiomycete Fungi. Yu J-H, editor. *PLoS One*. 2014 1 22;9(1):e86683.24466198
162. Chen W, Lee M-K, Jefcoate C, Kim S-C, Chen F, Yu J-H. Fungal Cytochrome P450 Monooxygenases: Their Distribution, Structure, Functions, Family Expansion, and Evolutionary Origin. *Genome Biol Evol*. 2014 7 1;6(7):1620–34.24966179
163. Qhanya LB, Matowane G, Chen W, Sun Y, Letsimo EM, Parvez M, Yu J-H, Mashele SS, Syed K. Genome-Wide Annotation and Comparative Analysis of Cytochrome P450 Monooxygenases in Basidiomycete Biotrophic Plant Pathogens. *PLoS One*. 2015 11 4;10(11):e0142100.26536121
164. Baroncelli R, Amby DB, Zapparata A, Sarrocco S, Vannacci G, Le Floch G, Harrison RJ, Holub E, Sukno SA, Sreenivasaprasad S, Thon MR. Gene family expansions and contractions are associated with host range in plant pathogens of the genus *Colletotrichum*. *BMC Genomics*. 2016;17(1):555.27496087
165. de Man TJB, Stajich JE, Kubicek CP, Teiling C, Chenthamara K, Atanasova L, Druzhinina IS, Levenkova N, Birnbaum SSL, Barribeau SM, Bozick BA, Suen G, Currie CR, Gerardo NM. Small genome of the fungus *Escovopsis weberi*, a specialized disease agent of ant agriculture. *Proc Natl Acad Sci U S A*. 2016 3 29;113(13):3567–72.26976598
166. Selker EU, Garrett PW. DNA sequence duplications trigger gene inactivation in *Neurospora crassa*. *Proc Natl Acad Sci U S A*. 1988 9;85(18):6870–4.2842795
167. Selker EU. Premeiotic Instability of Repeated Sequences in *Neurospora crassa*. *Annu Rev Genet*. 1990 12 1;24(1):579–613.2150906
168. Galagan JE, Calvo SE, Borkovich KA, Selker EU, Read ND, Jaffe D, FitzHugh W, Ma L-J, Smirnov S, Purcell S, Rehman B, Elkins T, Engels R, Wang S, Nielsen CB, Butler J, Endrizzi M, Qui D, Ianakiev P, Bell-Pedersen D, Nelson MA, Werner-Washburne M, Selitrennikoff CP, Kinsey JA, Braun EL, Zelter A, Schulte U, Kothe GO, Jedd G, Mewes W, Staben C, Marcotte E, Greenberg D, Roy A, Foley K, Naylor J, Stange-Thomann N, Barrett R, Gnerre S, Kamal M, Kamvysselis M, Mauceli E, Bielke C, Rudd S, Frishman D, Krystofova S, Rasmussen C, Metzenberg RL, Perkins DD, Kroken S, Cogoni C, Macino G, Catcheside D, Li W, Pratt RJ, Osmani SA, DeSouza CPC, Glass L, Orbach MJ, Berglund JA, Voelker R, Yarden O, Plamann M, Seiler S, Dunlap J, Radford A, Aramayo R, Natvig DO, Alex LA, Mannhaupt G, Ebbole DJ, Freitag M, Paulsen I, Sachs MS, Lander ES,

- Nusbaum C , Birren B . The genome sequence of the filamentous fungus *Neurospora crassa*. *Nature*. 2003 4 24;422(6934):859–68.12712197
169. Galagan JE , Selker EU . RIP: the evolutionary cost of genome defense. *Trends Genet*. 2004 9;20(9):417–23.15313550
 170. Tettelin H , Masignani V , Cieslewicz MJ , Donati C , Medini D , Ward NL , Angiuoli SV , Crabtree J , Jones AL , Durkin AS , DeBoy RT , Davidsen TM , Mora M , Scarselli M , Margarit y Ros I , Peterson JD , Hauser CR , Sundaram JP , Nelson WC , Madupu R , Brinkac LM , Dodson RJ , Rosovitz MJ , Sullivan SA , Daugherty SC , Haft DH , Selengut J , Gwinn ML , Zhou L , Zafar N , Khouri H , Radune D , Dimitrov G , Watkins K , O'Connor KJB , Smith S , Utterback TR , White O , Rubens CE , Grandi G , Madoff LC , Kasper DL , Telford JL , Wessels MR , Rappuoli R , Fraser CM . Genome analysis of multiple pathogenic isolates of *Streptococcus agalactiae*: Implications for the microbial “pan-genome.” *Proc Natl Acad Sci U S A*. 2005 9 27;102(39):13950–5.16172379
 171. Medini D , Donati C , Tettelin H , Masignani V , Rappuoli R . The microbial pan-genome. *Curr Opin Genet Dev*. 2005 12;15(6):589–94.16185861
 172. Strobe PK , Skelly DA , Kozmin SG , Mahadevan G , Stone EA , Magwene PM , Dietrich FS , McCusker JH . The 100-genomes strains, an *S. cerevisiae* resource that illuminates its natural phenotypic and genotypic variation and emergence as an opportunistic pathogen. *Genome Res*. 2015 5;25(5):762–74.25840857
 173. Yue J-X , Li J , Aigrain L , Hallin J , Persson K , Oliver K , Bergstrom A , Coupland P , Warringer J , Lagomarsino MC , Fischer G , Durbin R , Liti G . Contrasting evolutionary genome dynamics between domesticated and wild yeasts. *Nat Genet*. 2017 6;49(6):913–24.28416820
 174. Rokas A The effect of domestication on the fungal proteome. *Trends Genet*. 2008 12 10;25(2):60–3.19081651
 175. Gibbons JG , Salichos L , Slot JC , Rinker DC , McGary KL , King JG , Klich MA , Tabb DL , McDonald WH , Rokas A . The evolutionary imprint of domestication on genome variation and function of the filamentous fungus *Aspergillus oryzae*. *Curr Biol*. 2012 8 7;22(15):1403–9.22795693
 176. Steenwyk JL , Soghigian JS , Perfect JR , Gibbons JG . Copy number variation contributes to cryptic genetic variation in outbreak lineages of *Cryptococcus gattii* from the North American Pacific Northwest. *BMC Genomics*. 2016 9 2;17:700.27590805
 177. Ohm RA , Feau N , Henrissat B , Schoch CL , Horwitz BA , Barry KW , Condon BJ , Copeland AC , Dhillon B , Glaser F , Hesse CN , Kosti I , LaButti K , Lindquist EA , Lucas S , Salamov AA , Bradshaw RE , Ciuffetti L , Hamelin RC , Kema GH , Lawrence C , Scott JA , Spatafora JW , Turgeon BG , de Wit PJ , Zhong S , Goodwin SB , Grigoriev IV . Diverse lifestyles and strategies of plant pathogenesis encoded in the genomes of eighteen Dothideomycetes fungi. *PLoS Pathog*. 2012;8:e1003037.23236275
 178. Balesdent M-H , Fudal I , Ollivier B , Bally P , Grandaubert J , Eber F , Chèvre A-M , Leflon M , Rouxel T . The dispensable chromosome of *Leptosphaeria maculans* shelters an effector gene conferring avirulence towards *Brassica rapa*. *New Phytol*. 2013 5;198(3):887–98.23406519
 179. Stukenbrock EH , Jørgensen FG , Zala M , Hansen TT , McDonald BA , Schierup MH . Whole-genome and chromosome evolution associated with host adaptation and speciation of the wheat pathogen *Mycosphaerella graminicola*. *PLoS Genet*. 2010 12 23;6(12):e1001189.21203495
 180. Galazka JM , Freitag M . Variability of chromosome structure in pathogenic fungi-of “ends and odds.” *Curr Opin Microbiol*. 2014 5 15;20C:19–26.

Figure 1. Phylogenetic relationships of the Fungal Phyla and subphyla.

A phylogenetic tree from 434 conserved protein coding genes resolves the relationships of most of the known lineages of fungi. This tree is a simplified version of that presented in Spatafora et al. [44]. Phyla are presented in Bold and subphyla in regular type. The Chytridiomycetes and Monoblepharidomycetes represent lineages for which there is not a sub-phyla yet named.

Figure 2. Scatter plot showing relationship between genome size and gene count.

Genome size varies among subphyla of fungi with some of the smallest genomes in the Microsporidia and the largest currently sequenced genomes in the Agaricomycotina and Pezizomycotina. Primary data are gathered from genome information available at National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/>) and Joint Genome Institute Mycocosm (<https://jgi.doe.gov/fungi>) and archived in the 1KFG genome_stats github project (https://github.com/1KFG/genome_stats).