Fungal genomes and insights into the evolution of the kingdom

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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* (Agaricomyoctina), with a median gene count of 11,000 genes. Some of 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 *Ashyba*), 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* (Agaricomyoctina; 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 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 glucuronoxylo-mannogalactan [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 blakesleaanus* (Mucoromyoctina; 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 monoxygenase 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.

Figure Legends

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).

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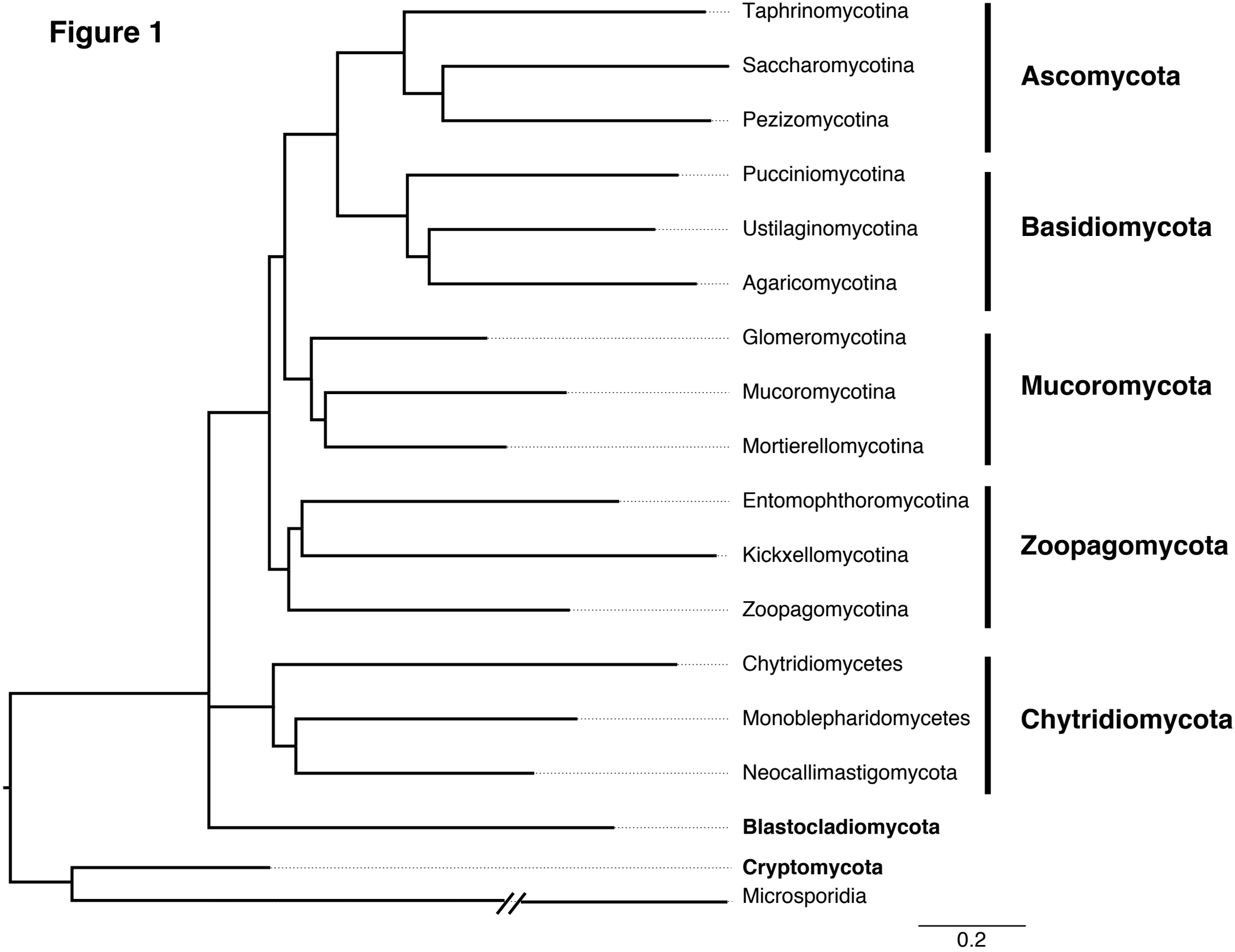
Figure 1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Mucoromycotina
Mortierellomycotina
Mucoromycota
Entomophthoromycotina
Kickxellomycotina
Zoopagomycotina
Zoopagomycota
Chytridiomycetes
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Cryptomycota
Microsporidia
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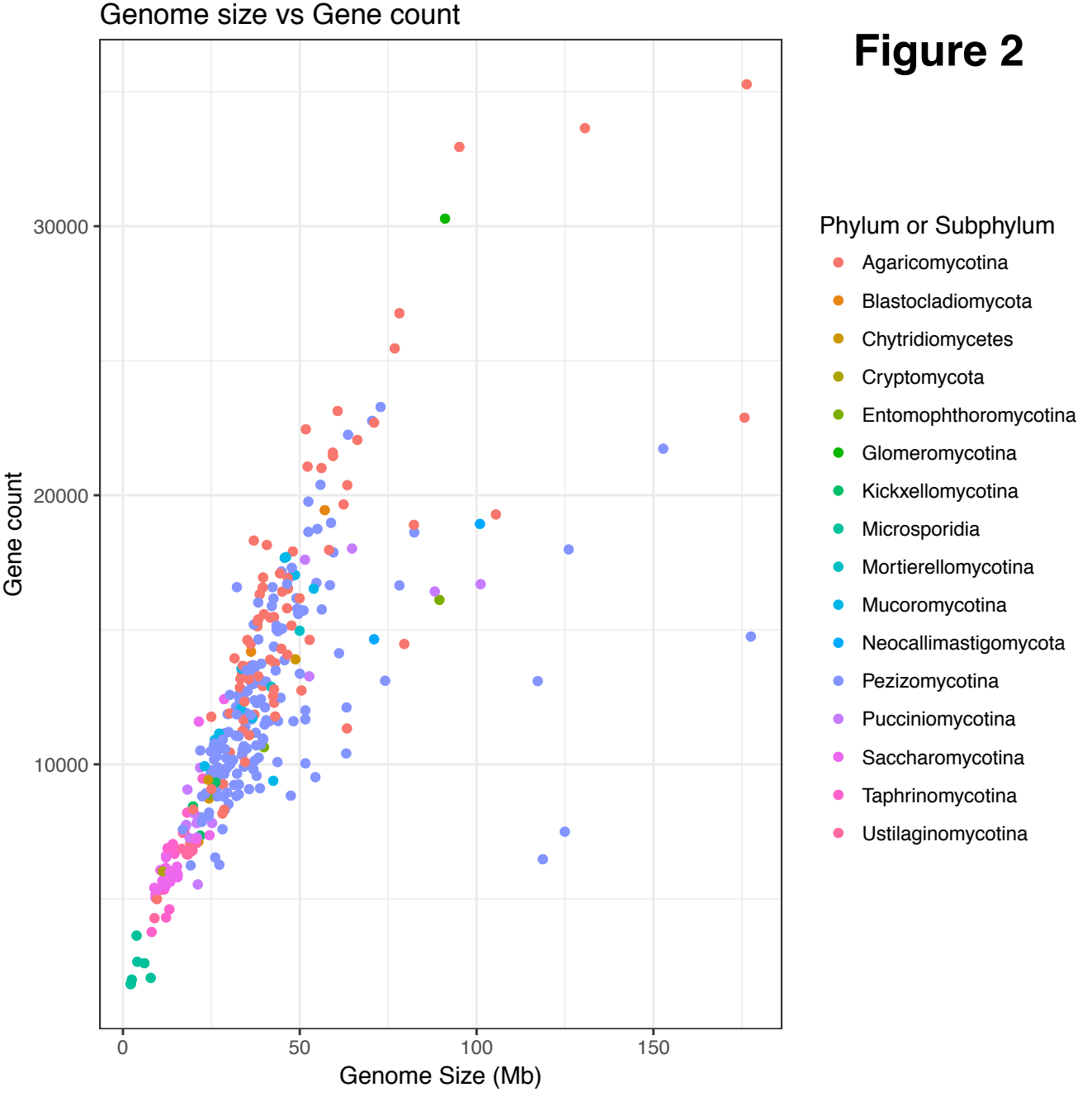
Figure 2


Genome size vs Gene count
Gene count
30000
20000
10000
0
50
100
150
Genome Size (Mb)
Phylum or Subphylum
Agaricomycotina
Blastocladiomycota
Chytridiomycetes
Cryptomycota
Entomophthoromycotina
Glomeromycotina
Kickxellomycotina
Microsporidia
Mortierellomycotina
Mucoromycotina
Neocallimastigomycota
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