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Fungal genomes tell a story of ecological adaptations

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ABSTRACT

One genome enables a fungus to have various lifestyles and strategies depending on environmental conditions and in the presence of specific counterparts. The nature of their interactions with other living and abiotic elements is a consequence of their osmotrophism. The ability to degrade complex compounds and especially plant biomass makes them a key component of the global carbon circulation cycle. Since the first fungal genomic sequence was published in 1996 mycology has benefited from the technolgical progress. The available data create an unprecedented opportunity to perform massive comparative studies with complex study design variants targeted at all cellular processes.

KEY WORDS: fungal genomics, osmotroph, pathogenic fungi, mycorrhiza, symbiotic fungi, HGT

Fungal ecology is a consequence of osmotrophy

Fungi play a pivotal role both in industry and human health (Fisher *et al.* 2012). They are involved in biomass degradation, plant and animal infections, fermentation and chemical industry etc. They can be present in the form of resting spores, motile spores, amebae (in Cryptomycota, Blastocladiomycota, Chytrydiomycota), hyphae or fruiting bodies. The same fungal species depending on environmental conditions and in the presence of specific counterparts can display various lifestyles and strategies for example entomopathogenic fungi are often encountered as leaf endosymbionts (Spatafora *et al.* 2007). Since fungi are involved in complex relationships with other organisms, their ecological repertoire is reflected in their genomes. The nature of their interactions with other organisms and environment is defined by their osmotrophic lifestyle. Nutrient acquisition and communication with symbionts and hosts are mediated by secreted molecules. Fungi possess complex repertoires of secreted molecules and membrane transporters efficiently transporting specific compounds in both directions (Richards

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& Talbot 2013). Their ability to degrade plant debris, especially lignin and cellulose makes them a key component of the global carbon circulation cycle**.** Organism adaptation is achieved by gene duplications leading to increased gene families. Expanded specific gene families result from adaptation towards a specific lifestyle, carbohydrate degrading enzymes are characteristic of plant related fungi whereas proteases of dermatophytes.

Fungal genomics and 1KF genomes

Fungi have been used as model organisms to study eukaryotic genetics for decades. Their compact genomes, well studied biology and availability of molecular tools made them ideal candidates for genome sequencing (a PubMed search results in 30932 articles related to "fungal genomes", July 2014). The genomic sequence of *Saccharomyces cerevisiae* published in 1996 was a milestone in mycology and genetics (Goffeau *et al*. 1996, Engel *et al*. 2014).

Currently the 1000 Fungal Genomes Project (1KF) is aiming at sequencing two representatives of each fungal family, everyone can nominate a sequencing candidate *via* a web service [http://genome.jgi.doe.gov/pages/fungi-1000-projects.jsf]. The available data create an unprecedented opportunity to perform massive comparative studies with complex study design variants targeted at all cellular processes.

Osmotrophic lifestyle and xenobiotic utilization

Fungal genomes are much more compact than plant and animal ones. Genes involved in a common metabolic pathway are often not only co-regulated by the same transcription factor, but also co-localized in the genome. In some cases this genomic proximity leads to gene cluster formation. Gene clusters are claimed as HGT (horizontal gene transfer) prone. Their direct acquisition leads to a straightforward evolutionary benefit and outcompeting other microbes (Richards & Talbot 2013). Since fungi are osmotrophs their adaptation to new ecological niches means developing strategies to degrade new substrates. Mechanistically this is often achieved by gene duplications with subsequent substrate specificity alterations of the resulting paralogs. As an example, the genome of *Ceriporiopsis subvermispora* shows its adaptation to lignin degradation in the expansions of laccases and manganese peroxidases (Fernandez-Fueyo *et al.* 2012)**.**

Gene organization, co-expression and co-regulation are essential when a metabolic pathway includes steps with toxic intermediates. Such pathways are sometimes conserved among distant evolutionary groups. Interestingly homologs of gene clusters with toxic intermediates which co-localize in fungi are often co-regulated in distant organisms, even in humans (McGary *et al*. 2013). It seems that clustering genes involved in a common pathway with toxic intermediates is selected for protection against the accumulation of such intermediates.

Genome size, genome richness, compactness

According to a growing body of population genetics evidence increased genome sizes result from decreased effective population size in the course of evolution of eukaryotic populations. The drop in effective population size leads to

continuously growing complexity of genomes with expanded gene families, genes fragmented by introns and surrounded by regulatory regions and mobile elements which eventually results in greater overall genome sizes. All genome components seem to expand together. However, in fungi the coding genome size is less variable than other genome components, with gene numbers between six and twenty thousand. Fungi vary in genome size and genome compactness. *Tuber melanosporum* (Pezizomycotina) an ectomycorrhizal forming fungus has a 125 Mb long genome with many transposable elements (Martin *et al*. 2010) whereas plant pathogenic *Taphrina deformans* (Taphrinomycotina) has only a 14 Mb genome (Cissé *et al*. 2013). Micorosporidia have extremely compact and reduced genomes which can be treated as a course book example of adaptation to obligate intracellular parasitism (Cuomo *et al*. 2012). The peculiarities of obligate pathogen genomes cause problems in phylogeny reconstruction. Microsporidia position within fungi has been long discussed and currently they are considered as one of basal fungal lineages together with Cryptomycota (James *et al*. 2013). Genome sizes and gene numbers can be immediately elevated as a consequence of a whole genome duplication (WGD). The ohnologs (paralogs resulting from WGD) are known to evolve in an asymmetric manner, often leading to gene loss or to neofunctionalizing. WGDs have been detected in the evolutionary history of distant fungal lineages for example in *Rhizopus delemar* (Mucorales) (Ma *et al*. 2009) and *Saccharomyces cerevisiae* (Saccharomycetales) (Byrne & Wolfe 2007).

At least some fungi are said to possess a two-speed genome i.e. a genome with housekeeping genes and the other genome with additional features, encoding specific effectors. The former, primary genome is more compact, has a few and usually inactive mobile elements and introns. The latter, accessory genome is less gene dense, encodes many species/strain specific genes, has more mobile elements, often from younger families, sometimes still active and intact. As an example rust fungi possess one of the biggest genomes among fungi, with areas abundant in mobile elements and short genes coding effector proteins.

Effector proteins

Short, secreted, cysteine rich proteins are said to mediate interactions with a host organism either a plant or an animal. Effectors play an immunomodulatory role, both in pathogenic and symbiotic fungi, they can suppress host immune response and thus facilitate tissue colonization (de Jonge *et al*. 2011, Schmidt & Panstruga 2011). One of the plant defence mechanisms is *via* jasmonic acid and mycorrhizal fungi like *Laccaria bicolor* (Agaricales) can promote mutualism by blocking the signalling (Plett *et al*. 2011). The repertoire of effector proteins evolves much faster than of housekeeping genes because it is in a constant 'arms race' with the host immune system. These effectors are often clustered with transposons which alter their expression. Host adaptation and host switching is often reflected in encoded effector protein composition. Between closely related taxa of *Nectria haematococca* and *Fusarium oxysporum* this adaptation is achieved by proteins encoded on

supernumerary chromosomes carrying, among others, host specific effectors and mobile elements (Coleman *et al*. 2009, Ma *et al*. 2010). Conditionally dispensable chromosomes and lineage specific chromosome regions are rich in repeat sequences, unique and duplicated genes and reflect the species habitat/niche.

Mobile elements in fungal genomes

Lynch (Lynch & Conery 2003) postulated that overall genome size correlated with mobile element content and decreasing effective population size. In fungi, the genome size indeed correlates well with the overall mobile element content. Transposons (TE) are DNA fragments capable of moving to new locations within a single genome in a process called transposition. Genomes and transposons have probably coevolved for all their history. TEs are usually dormant components of the genome, activated under stress conditions (Capy *et al*. 2000, Abe *et al*. 2009). Epigenetic silencing probably evolved to control transposition (Hua-Van *et al*. 2011). Transposons influence the expression of genes both in *cis* and in *trans*, alternate splicing, can lead to gene inactivation and become a source of new exons. Being a target of epigenetic machinery they change even the chromatin state of huge parts of a genome. Fungi defend their genomes by means of repeat-induced point mutation (RIP), meiotic silencing and quelling (Aramayo & Selker 2013). This richness of mechanisms reflects the significance of maintaining balance between different genome components. Studies of transposons at the kingdom level were limited to the best studied taxonomic groups and transposon types, LTR retrotransposon (Muszewska *et al*. 2011), YR retrotransposons (Muszewska *et al*. 2013), non-LTR retrotransposons (Novikova *et al*. 2009). These and other analyses have showed that plant pathogens often possess large and repeat-rich genomes (*Magnaporthe grisea*, *Mycosphaerella graminicola*, *M. fijensis*, *Blumeria graminis*) (Raffaele & Kamoun 2012). This rule is not universal and there are well studied examples such as *Ustilago maydis* with a small genome almost devoid of repeats. Transposons are involved in adaptation to new hosts and lead to altered virulence by changing genomic regions with clustered effector and avirulence genes (Kang *et al*. 2001, Van de Wouw *et al*. 2010). Transposons seem to provide an advantage in host-pathogen 'arms race' (Raffaele & Kamoun 2012). In the genome of *Pyrenophora tritici-repentis* TEs mediated adaptation towards pathogenicity by contributing to novel gene creation, effector diversification, facilitating horizontal gene transfer events and transduplication (Manning *et al*. 2013). There seems to be a link between symbiotic lifestyle in *Amanita* species and TE proliferation (Hess *et al*. 2014).

Horizontal gene transfer

HGT is a major force shaping prokaryotic genomes, in Eukaryota its impact is less pronounced. However, HGT from and to fungi has been reported in multiple studies. Unique mechanisms such as anastomosis and parasexual processes as well as close relationships, either symbiotic or pathogenic, of fungi with other organism provide additional ways for HGT within the fungal

kingdom. Fungi-like oomycetes have acquired many fungal genes enabling them to utilize compounds which are difficult to degrade (Richards & Talbot 2013). It is expected that genes coding genes used for nutrient acquisition will be transferred more successfully compared to those coding machinery involved in genetic material maintenance and processing. This bias towards niche-related genes is expected, because the housekeeping genes are involved in complex interaction networks and a newly acquired gene has to fit into the genetic environment of an acceptor. It is an open question now whether HGT between fungi is more common than from prokaryote to fungi (Richards 2011). There is a significant number of documented prokaryote to fungi transfers (Marcet-Houben & Gabaldón 2010). There are cases of entire biosynthetic pathway transfer between fungi (Richards 2011). *Fusarium* species have transferred fumonisin biosynthetic gene cluster many times in evolution (Proctor *et al*. 2013). HGT is known to occur rarely in Eukaryota, but co-transfers functionally link genes and therefore plays a role in adaptation to a certain niche.

Mobile elements and speciation

Mobile elements accumulation and proliferation leads to increasing incompatibility between taxa. The latter is one of the mechanisms underlying speciation, leading to the formation of separated taxa. The concept of species is one of the most discussed issues in theoretical biology (Taylor *et al*. 2000). The overall pattern of TEs in a species seems to be fixed with single elements being activated and widespread. The differences in TE content can be analysed not only in relation to the ratio of each group of elements in the total TE content, but also to the abundance of each major type of elements, e.g. recent separation of *Paracoccidioides brasiliensis* and *P. lutzii* sibling species upon genomic and physiological analyses (Teixeira *et al*. 2009, Desjardins *et al*. 2011). The aforementioned example of *P. brasiliensis* is an argument in favour of considering TEs as components of the definition of a species. The degree of divergence among strains of a species of interest has to be individually defined taking into account data from related taxa.

Sexual reproduction

Sexual reproduction is beneficial in many ways, it helps to get rid of deleterious mutations and fix beneficial mutations, to escape from pathogens, can be a source of genetic diversity and in consequence is widely spread among Eukaryota. However, this comes at cost of finding a mating partner, transmitting only 50% of own genetic material and breaking apart well adapted genomic configurations (Heitman *et al*. 2013). In contrast to animals, fungi seldom are obligatory sexual, usually they can reproduce asexually for many generations and sexually from time to time. Arbuscular mycorrhiza forming fungi have been considered asexual for a long time. However, genomic studies showed they have key components of the meiotic machinery (Halary *et al*. 2011). Recently mating type high mobility group (MATA-HMG) domain proteins which are sex determinants and play key roles in sexual reproduction in many fungal lineages such as Mucoromycotina, Euascomycotina, in the *Candida* clade,

have been identified in *Rhizophagus irregularis* (Glomeromycota). *R. irregularis* not only possesses MATA-HMG coding genes, but actually has an elevated number of MATA HMG copies (Riley *et al.* 2014).

Sexual reproduction models in fungi include tetrapolar, bipolar and unipolar systems (Heitman *et al*. 2013). The mating type loci can be very simple ranging from >1000 bp long loci with a single homeodomain transcription factor (TF) to 120 kb long genomic regions in *Cryptococcus neoformans*. The best studied bipolar system was described in *Sacharomyces cerevisiae.* It consists of one haploid a cell with an a locus coding a single homeodomain transcription factor, and another haploid α cell with an α locus coding two TFs, a homeodomain TF which forms an a-α heterodimer during mating and another homeodomain TF which regulates α-specific genes. A tetrapolar system has been described for *Ustilago maydis* with two different, unlinked mating type loci *a* and *b*, *a* coding for homedomain TFs, and *b* for pheromone and pheromone receptors. The *a* locus is biallelic and the *b* locus is multiallelic which results in a multitude of possible combinations. Adaptation towards pathogenicity leads to convergent changes from ancestral tetrapolar systems to bipolar systems and occurred repeatedly in Basidiomycota evolution in e.g. *Ustilago hordei*, *Malassezia restricta* and *M. globosa* and in *Filobasidiella* taxa. Moreover, unisexual reproduction seems to be widespread in pathogens, and can lead to diverse progeny even if only one parent was present (Heitman *et al*. 2013). There is a variable balance between inbreeding and outcrossing, and in animal pathogens it seems to be favourable to enhance inbreeding. According to Heitman and colleagues (2013) unisexual reproduction not only generates genetic diversity *de novo* but eliminates the costs of sexual reproduction and evolved repeatedly.

Conclusions

Fungi possess a combination of features among others osmotrophic nutrient acquisition, close interactions with other organisms, complex metabolic potential, variable reproduction models, which together have to be reflected in their genomes. Recent advancement in sequencing has revealed more and more fascinating individual stories and showed both common and specific adaptations towards particular ecological niches. More genetic mechanisms underlying fungal ecological adaptations will be elucidated with the progress of functional genomics studies.

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Streszczenie

Grzyby odgrywają zasadniczą rolę w ekosystemach jako patogeny, saprotrofy i symbionty. Ich wszechstronne zdolności metaboliczne czynią z nich kluczowe ogniwo w obiegu węgla w przyrodzie. Dla człowieka stanowią głównie źródło infekcji, ale również zyskują na znaczeniu w biotechnologii (Fisher *et al*. 2012). Grzyby są obecne

w naszym otoczeniu w formie zarodników, pełzaków, grzybni i owocników. Te same gatunki grzybów w zależności od warunków otoczenia mogą prezentować rożne formy morfologiczne i tworzyć różne relacje z otoczeniem, na przykład owadobójcze grzyby są często spotykane jako endosymbionty roślin (Spatafora *et al*. 2007). Całe to bogactwo znajduje odzwierciedlenie w genomach grzybów. Osmotroficzny tryb życia grzybów narzuca charakter interakcji grzybów z otoczeniem, która odbywa się przy pomocy wydzielanych na zewnątrz enzymów rozkładających pożywienie, białek efektorowych oraz toksyn wpływających na inne organizmy. Grzyby posiadają złożone kompozycje wydzielanych cząsteczek oraz transportery błonowe przystosowane do efektywnego przenoszenia związków chemicznych w obu kierunkach (Richards & Talbot 2013). Zdolność do rozkładania ligniny i celulozy odpowiada w dużej mierze za sukces ewolucyjny grzybów. Adaptacja organizmu do nowego ekosystemu zwykle przebiega poprzez duplikację genów z ich późniejszymi asymetrycznymi zmianami prowadzącymi do szybkiej zmiany specyficzności substratowej jednego z paralogów. Wielokrotne duplikacje jednej grupy genów prowadzą do rozrostu rodziny kodowanych przez nie białek i rozszerzenia zakresu możliwości np. rozkładanych przez nie wariantów substratów. Zwiększenie liczby genów związanych z metabolizowaniem danej grupy substratów jest jednym z podstawowych sposobów adaptacji do danej niszy ekologicznej widzianej z perspektywy genomu. Charakterystyczne więc dla grzybów związanych z roślinami będzie kodowanie licznych enzymów degradujących węglowodany, a dla dermatofitów – proteazy i lipazy. Kolejnym poziomem adaptacji patogenów/symbiontów jest zmiana profilu ekspresji genów i stały „wyścig zbrojeń" z gospodarzami. Ponadto geny te często sąsiadują z transpozonami, w obrębie szybciej ewoluującej części genomu. Geny związane z metabolizowaniem ksenobiotyków częściej ulegają też horyzontalnemu transferowi genów aniżeli geny metabolizmu podstawowego. Inna wyróżniającą grzyby cechą jest posiadanie różnorodnych modeli rozmnażania płciowego nawet pomiędzy spokrewnionymi gatunkami. Model rozmnażania jest jednym z ważniejszych sposobów dostosowania do trybu życia. Rozmnażanie jednopłciowe pojawiało się wielokrotnie w ewolucji grzybów i wydaje się być adaptacją do patogennego trybu życia.