Fungal evolution: major ecological adaptations and evolutionary transitions

Miguel A. Naranjo-Ortiz and Toni Gabaldón

ABSTRACT

Fungi are a highly diverse group of heterotrophic eukaryotes characterized by the absence of phagotrophy and the presence of a chitinous cell wall. While unicellular fungi are far from rare, part of the evolutionary success of the group resides in their ability to grow indefinitely as a cylindrical multinucleated cell (hypha). Armed with these morphological traits and with an extremely high metabolical diversity, fungi have conquered numerous ecological niches and have shaped a whole world of interactions with other living organisms. Herein we survey the main evolutionary and ecological processes that have guided fungal diversity. We will first review the ecology and evolution of the zoosporic lineages and the process of terrestrialization, as one of the major evolutionary transitions in this kingdom. Several plausible scenarios have been proposed for fungal terrestrialization and we here propose a new scenario, which considers icy environments as a transitory niche between water and emerged land. We then focus on exploring the main ecological relationships of Fungi with other organisms (other fungi, protozoans, animals and plants), as well as the origin of adaptations to certain specialized ecological niches within the group (lichens, black fungi and yeasts). Throughout this review we use an evolutionary and comparative-genomics perspective to understand fungal ecological diversity. Finally, we highlight the importance of genome-enabled inferences to envision plausible narratives and scenarios for important transitions.

Key words: fungi, ecological adaptations, evolutionary transitions, fungal niches, fungal terrestrialization, fungal diversification.

CONTENTS

I. Introduction ..............................................................1444
II. In the beginning: early fungal evolution ..................................................1444
III. Down to earth: terrestrialization in fungi ............................................1445
IV. Fungi and other microbial eukaryotes ..................................................1448
   (1) ‘Fungus fungo lupus’: mycoparasitism in fungi ..................................1448
   (2) Fungi and protozoans ......................................................................1450
V. Fungi and animals ............................................................................1452
   (1) Overview ..................................................................................1452
   (2) Obligate parasites of animals .......................................................1453
   (3) Facultative parasites of animals ......................................................1454
   (4) Fungal commensals of animals .......................................................1456
VI. The fungus–plant biome: ecological interactions between plants and fungi ...............1457
   (1) Overview ..................................................................................1457
   (2) Mycorrhizae and plant commensal associates ................................1457
   (3) Plant parasitism ...........................................................................1458
   (4) Wood rot fungi ............................................................................1460
VII. More than the sum of their parts: lichenized fungi ................................1460

* Address for correspondence (Tel: +34 616 953 333; E-mail: tgabaldon@icrea.cat).
I. INTRODUCTION

The kingdom Fungi is a highly diverse clade of eukaryotes found in virtually all environments, particularly in terrestrial ecosystems (Richards, Leonard & Wideman, 2017; Stajich, 2017). Fungi play key roles in nutrient cycling, can act as predators, pathogens and parasites of myriad other organisms, and can be found living in symbiotic associations with plants, algae, animals and other organisms. Some important groups of fungi (mostly mushrooms and lichens) produce macroscopic structures that have been the focus of extensive morphological, cytological and biochemical studies (Lawrey & Diederich, 2009; Taylor & Ellison, 2010; de Mattos-Shipley et al., 2016; Grube & Wedin, 2016). Outside these groups, most fungi have been traditionally studied using culture-based microbiological techniques or by assessing the symptoms and specialized structures they produce on their hosts or symbiotic partners. During the past two decades, the genomic revolution has positively impacted the field of mycology, which has rapidly and enthusiastically embraced a comparative genomic paradigm to an extent that is still rare in other disciplines (Cuomo & Birren, 2010). The advent of genome and transcriptome sequencing has enabled the study of virtually any fungal group, and this has been reflected in an explosion of research covering a growing list of fungal species from diverse lineages. Last, but not least, environmental sequencing studies are revealing a new dimension of fungal biology. Barcoding-based approaches have been used in the last two decades to study the diversity of particular components of environmental fungal communities, such as ectomycorrhizal fungi (Lillevik et al., 2002; Landeweert et al., 2003; Cox et al., 2010); or to assess fungal composition in particular environments (Tedersoo et al., 2014; Xu, 2016; Yahr, Schoch & Dentinger, 2016). Mycologists have started to embrace the use of single-cell-based techniques, although tentatively due to incompatibilities of filamentous growth with cell-sorting approaches (Ahrendt et al., 2018). Each of these approaches presents specific limitations, but collectively they provide an emerging picture of where fungi are, who they are, and how they have become what they are.

Most fungal species live as a mycelial thallus, a cylindrical syncitium with indefinite apical growth encased in a chitinous cell wall and often compartmentalized by perforated septa (Richards, Leonard & Wideman, 2017). Fungi generally grow through solid substrates, using extracellular enzymes and brute force to dig into the substrate and exploit the resources in their surroundings. In addition, they take control of their territory by secreting toxic compounds, in chemical warfare with other microbes. Fungi have a well-developed secretome that allows them to extract nutrients, even from highly polymerized and often very hydrophobic compounds, such as cellulose or lignin, which is very difficult for other microbes (Richards & Talbot, 2013; Boddy & Hiscox, 2016; Hiscox, O’Leary & Boddy, 2018). Fungi can propagate over long distances by producing non-motile spores that may or may not be the product of mating between two compatible hyphae (Golan & Pringle, 2017). We will refer to these general features as the mould lifestyle. Despite being widespread, this lifestyle is not ancestral within the kingdom (Spatafora et al., 2017; Stajich, 2017) and fungi display many other forms of cellular organization and ecological lifestyles (Richards, Leonard & Wideman, 2017). Nevertheless, the mould paradigm is useful as a reference point from which to discuss morphological and ecological variations present across the kingdom. In this review, we synthesize current knowledge on the major ecological adaptations and evolutionary transitions within fungi. We define an evolutionary transition as the acquisition – within a lineage – of a new, sufficiently distinct lifestyle from a previous state. Well-known examples of such transitions include the acquisition of a parasitic lifestyle from free-living ancestors, the establishment of symbiosis (e.g. lichens), or radical changes in body-plan or cellular organization. When possible, we place such transitions within an evolutionary framework, explaining how zoosporic fungi evolved from motile eukaryotic parasites to moulds, and how from those two lifestyles different groups of fungi have shaped their relationships with other groups of organisms and have adapted to novel ecological niches. We focus on describing phenotypic and genomic generalities, taxonomic diversity, evolutionary trends and culture-independent environmental information for each of the discussed ecological lifestyles.

II. IN THE BEGINNING: EARLY FUNGAL EVOLUTION

Inferring the potential lifestyle of the last common fungal ancestor (LCFA) is challenging. The sister group to Fungi, the Nuclearida, are amoeboid protozoans that are common in marine environments, according to metagenomic studies (del Campo & Ruiz-Trillo, 2013; Del Campo et al., 2015). This, together with the age of the group, which pre-dates fossil evidence of terrestrial biota in most molecular dating analyses (Berbee, James & Strullu-Derrien, 2017), points to a likely marine origin for fungi. However, all known extant fungal lineages are apparently primarily continental, either truly terrestrial or associated with non-marine water.
Evolutionary and ecological transitions in fungi

III. DOWN TO EARTH: TERRESTRIALIZATION IN FUNGI

The most definitive evolutionary novelty within Fungi is the adaptation to land environments (terrestrialization), which involved the development of hyphal growth and the loss of the flagellum (Fig. 1). The development of the hypha likely reflects either the necessity to infect much larger organisms or to increase the surface of influence within a saprotrophic lifestyle. The ability to secrete digestive enzymes and to express abundant membrane transporters preferentially at the hyphal tips, can be understood as a direct consequence of an ancestral pillaging lifestyle of organisms that had to break into other living structures to obtain nutrients. In this regard, the uncoupling of calcium metabolism from the external medium shown by Fungi (Liu et al., 2015; Halling et al., 2016) could be interpreted as an adaptation to break into other cells, where the concentration of free Ca2+ is too low to constitute a reliable source. Specialized Ca2+ homeostasis adaptations are known for other unrelated intracellular parasites, such as Leishmania (Benaim & Garcia, 2011), Toxoplasma (Arrizabalaga & Boothroyd, 2004; Masek et al., 2007; Moreno, Ayong & Pace, 2011) and Plasmodium (Camacho, 2003; Moreno, Ayong & Pace, 2011).

The hypha of most filamentous fungi is organized around an organelle called the Spitzenkörper (SPK) (Steinberg, 2007; Arkowitz & Bassilana, 2011; Lin et al., 2014; Riquelme & Sánchez-León, 2014; Takeshita, 2016; Steinberg et al., 2017; Riquelme et al., 2018). The SPK is composed of a collection of vesicles originating in the Golgi apparatus that contain the enzymes, lipids and polysaccharides required for the synthesis of membranes and the cell wall. Surrounding the SPK are the polarisome and the exocyst. The polarisome is a series of proteins that organize cytoskeletal components and regulate cytoskeleton-mediated transport of vesicles (Lin et al., 2014; Riquelme et al., 2018). The exocyst, on the other hand, contains components that regulate the flux of vesicles to exocytic routes (Lin et al., 2014; Takeshita, 2016; Steinberg et al., 2017; Riquelme et al., 2018). These structures maintain the directionality of hyphal growth, regulate exocytosis of SPK components, modulate Ca2+ signalling and remodel the cell wall, among other functions. Hyphal growth studies reveal the conservation of this molecular machinery across all Dikarya, but information outside these groups is very limited. For instance, most zygomycetous fungi show a less-organized aggregation of vesicles named the apical vesicle crescent (AVC) (Fisher & Roberson, 2016). This structure has been studied mostly using electron microscopy, and ontological equivalence between SPK and AVC components is poorly known (Roberson et al., 2011; Henk & Fisher, 2012; Fisher et al., 2018). The SPK seems to be present in Basidiobolus (Roberson et al., 2011) and Conidiobolus (Fisher et al., 2018), which are early-diverging lineages within the Entomophthoromycotina. Members of the Blastocladiomycota (e.g. Allomyces, Blastocladia) also have a morphologically recognizable SPK (Vargas, Aronson & Roberson, 1993; Srinivasan, Vargas & Roberson, 1996;
Fig. 1. Phylogenetic tree showing main ecological transitions across the non-Dikarya fungi. Symbols on the right indicate that the transition has occurred within the group.

McDaniel & Roberson, 1998; James, Porter & Martin, 2014). The presence of the SPK in these lineages suggests that the common ancestor of all terrestrial fungi could have had an SPK that was lost or modified to a AVC in zygomycetous fungi, although it is impossible to rule out an independent origin of the SPK in these lineages.

Several possible evolutionary scenarios could explain how Fungi colonized land, which in turn triggered their explosive diversification. Solving this question will require improving our knowledge on the microbial composition of early soils, and more precise dating of key events such as land plant diversification, and the radiation of terrestrial fungi. We refer to these alternative hypotheses as the ‘green’, ‘brown’ and ‘white’ scenarios for the terrestrialization of fungi, based on their emphasis on plants, soils, and ice, respectively (Fig. 2).

The ‘green’ scenario was formulated in its modern form by Lücking et al. (2009), although it was discussed in similar terms much earlier. For example, Savile (1969) proposed that fungi would have had to exist as parasites of vascular plants to resist dehydration during the early stages of land colonization. The ‘green’ scenario proposes that Fungi co-evolved with the ancestors of land plants. Arriving from freshwater bodies as parasites of green algae, and from the margins of rivers and lakes, they conquered the terrestrial world, following plants in their adaptations to terrestrial environments. This was likely accompanied by increased complexity (first rhizoids, later hyphal growth) as multicellularity became common in the Streptophyta. Of note, land plants and the unicellular green algae Trebouxia contain in their genome evidence of several ancient horizontal gene transfers of putative fungal origin.
Evolutionary and ecological transitions in fungi

Fig. 2. Schematic representation of the three hypothesis for fungal terrestrialization. The ‘green’ scenario implies that terrestrialization of fungi was dependent on terrestrialization in green plants, probably Streptophyta. The ‘brown’ scenario assumes that zoosporic fungi acquired saprotrophic habits and colonized sediments or damp land, prior to the loss of the flagellum, followed by development of hyphal growth and complete terrestrialization. The ‘white’ path implies that zoosporic fungi adapted to frozen environments that acted as an intermediate between aquatic and terrestrial environments.

(Emiliani et al., 2009; Richards et al., 2009; Beck et al., 2015); and the genes required for symbiosis with fungi also show homology in green algae (Delaux et al., 2015). In some cases, these transferred genes have been functionally linked to adaptations to dry land. While this implies that Fungi were present when green algae started to colonize land, it does not show that they arrived together.

An alternative hypothesis involves co-evolution with soil itself (Taylor & Osborn, 1996), which we refer to as the ‘brown’ scenario. This scenario is based on the idea that emerged lands likely had microbial crust-like communities dominating the landscape, including bacteria and probably also eukaryotic algae and protozoans (Astafieva & Rozanov, 2012; Wu et al., 2014). Under this scenario, Fungi would have colonized these protosoils, rapidly splitting between a lineage associated with Streptophyta (Mucoromycota, Glomeromycota and Dikarya) and a lineage of parasites of protists (Zoopagomycota). It is important to note that microfossils of testate amoebae, that today inhabit many environments including soils, are known from the Proterozoic era (Porter & Knoll, 2000; Knoll, 2014). Hence, it is conceivable that amoebopathogenic Zoopagomycota were already parasites of such amoebae, although it is very unlikely that we will find compelling fossil evidence to confirm this. Ediacaran circular fossils have been proposed to represent microbial mats (Grazhdankin &
et al., 2007; LaFlamme et al., 2011), and are similar to certain contemporary communities known to harbour fungi (Cantrell & Duval-Pérez, 2012; Cantrell et al., 2013). Other authors claim these fossils are from lichens and slime moulds (Retallack, 2012), suggesting an already well-developed terrestrial microbial ecosystem.

We here put forward an additional hypothesis to explain fungal terrestrialization. This ‘white’ scenario involves icy environments as facilitators of the transition from water to terrestrial environments in fungi. Since icy environments are formed by abiotic factors, it is safe to assume that they existed before the divergence of terrestrial Fungi. The general assumption that low temperatures impose extreme conditions to microbial life is a misconception. Fungi show lower diversity at the poles than in the tropics, but this decrease is not as pronounced as it is for plants and animals (Tedersoo et al., 2014). Additionally, this trend is not universal across all fungal lineages, with some even showing higher diversity in polar areas. Unlike thermophilic environments, these microniche are inhabited by microbial genera that are also found in temperate conditions (Boetius et al., 2015; Anesio et al., 2017), suggesting that adaptation to low temperatures in microbes is an evolutionarily easy step. The main challenge in such environments seems to be liquid water limitation and, to a lesser degree, irradiation, rather than temperature. Both stresses are also common in soils. As compared to the water column, icy environments are much more heterogeneous and unstable (Boetius et al., 2015; Smith et al., 2016; Anesio et al., 2017; Hotaling, Hood & Hamilton, 2017), a feature shared with soils. Certain microniche in icy environments, such as highly saline brine channels and cryoconites caused by exclusion of solutes from the ice crystal, contain an impressive microbial diversity (Boetius et al., 2015; Gokul et al., 2016; Anesio et al., 2017). Such environments are nutrient rich, spatially limited, and might be temporary, depending on external conditions. Environmental 18S ribosomal RNA (rRNA) sequencing from five ice-covered lakes in the Antarctic McMurdo Valleys recovered a total of 1313 fungal operational taxonomic units (OTUs) in a community dominated by Chytridiomycota and Rozellidea, but also including Ascomycota, Basidiomycota, Blastocladiomycota and zygomycetous fungi (Rojas-Jimenez et al., 2017). Analyses of six replicates in two Antarctic continental brines separated by a thin ice layer recovered 600 OTUs that clustered in two clearly different communities with very little overlap (Borruso et al., 2018). This suggests that ice environments might have huge spatial heterogeneity. Ice masses contain important snow algal communities (Anesio et al., 2017; Davey et al., 2019) that might have acted as hosts or sources of necromass for zoosporic ancestors of terrestrial fungi (Kasotská et al., 2005; Boetius et al., 2015; Duran et al., 2017; Hotaling, Hood & Hamilton, 2017). Zoosporic fungi can propagate easily through semi-melted ice surfaces, and even modern icy environments, such as periglacial soils or arctic seas, contain an unsuspected abundance and diversity of zoosporic lineages (Freeman et al., 2009; Hassett & Gradinger, 2016; Råmå et al., 2017).

Even cryptoendolithic communities in antarctic dry valleys, commonly regarded as one of the harshest environments on Earth (Scalzi et al., 2012), harbour a considerably diverse community spanning several hundreds of detectable OTUs that include mostly lichen-forming Ascomycota, black fungi and yeasts forms of both Ascomycota and Basidiomycota (Colecne et al., 2018).

Finally, the estimated dates of radiation of fungal terrestrial lineages (Taylor & Berbee, 2006; Berbee & Taylor, 2010; Prieto et al., 2013b; Knoll, 2014; Lutzeni et al., 2018) overlap with the Precambrian glaciations, a period also known as ‘Snowball Earth’ or the Cryogenian (Hoffman et al., 2017). This period also witnessed the radiation of at least two clades of non-Streptophyta terrestrial algae (Trebusiophyceae and Trentepohliiales) (Lutzeni et al., 2018). From these observations, we propose the following course of events for fungal terrestrialization: (i) Snowball Earth scenarios created a diversification of microbial niches. This is not a necessity, since ice environments are not exclusive to ice ages, but the timing of the diversification suggests that it might have played an important role. (ii) Fungi arrived in ice environments as zoosporic predators of algae. (iii) Highly osmotic microniche and accumulation of algal necromass favoured the development of hyphal growth and true osmotrophy to exploit these nutrient sources effectively even in limited time windows. (iv) Intermittent conditions favoured the development of resistant resting spores. These conditions would be much longer under glaciation scenarios. Flagellar motility was lost. (v) Fungi, adapted to living under water limitation in icy environments, were then able to colonize soil environments.

In summary, the three hypothesized scenarios for the origin of fungal terrestrialization focus on different biotic or abiotic factors that could have acted sequentially or in combination. Given the lack of a clear fossil record, the evidence supporting each of these scenarios is necessarily only circumstantial and mostly based on extrapolations from our knowledge of modern environments. A common factor to all three scenarios is that terrestrialization of fungi must have followed or been contemporary with that of other eukaryotic groups (amoebae, algae, or plants). After terrestrialization, relationships with other groups of organisms would have allowed the radiation of the main terrestrial lineages, with Zoopagomyctota being primarily associated with other microbes and metazoa, and the clade Glomeromyctota + Mucoromyctota + Dikarya being primarily associated with plants.

IV. FUNGI AND OTHER MICROBIAL EUKARYOTES

1) ‘Fungus fungo lupus’: mycoparasitism in fungi

Fungi are voracious microbes that are able to attack and digest virtually any kind of living structure, including other
Evolutionary and ecological transitions in fungi

The ability to infect other fungi appeared very early. Mycoparasitic associations are already found in the oldest unequivocal fungal fossils, in the Rhynie Chert, an early Devonian deposit formed around 410 million years ago (Hass, Taylor & Remy, 1994). However, this lifestyle probably appeared earlier, as mycoparasitism is widespread among early-diverging fungi (Fig. 3). Rozella (Rozellidea) parasitizes both fungi and Oomycetes (Gleason et al., 2012). Mycoparasites have been reported within the Chytridiomycota and the Blastocladiomycota, albeit with limited described diversity (Hajek et al., 2013; Powell & Letcher, 2014). The families Piptocephalidaceae and Sigmoidomyctaceae within the Zoopagomycotina, as well as the Dimargantiales within the Kickxellomycotina, are richly populated with mycoparasitic species (Tanabe et al., 2000; Benny, Humber & Voigt, 2014; Benny et al., 2016).

The genomes of several of these biotrophic mycoparasites have been recently obtained through the use of single-cell sequencing techniques, a necessity given their usually small thalli (Ahrendt et al., 2018). Many of these organisms have lost genes from important metabolic pathways, such as biotin, polyamines, assimilatory sulfate or the tricarboxylic acid cycle. Members of the Mucoromycotina are also common parasites of other fungi, both as a necrotrophs and biotrophs (Benny, Humber & Voigt, 2014). Parasitic Agaricomycetes usually infect the fruiting bodies of other fungi, although species infecting hyphae or conidia are also known (Tzean & Estey, 1978; Jeffries, 1995). Mycoparasitism is widespread within Pucciniomycotina, where it seems to be an ancestral lifestyle (Aime, Toome & McLaughlin, 2014; Wang et al., 2015b; Oberwinkler, 2017) (Fig. 3). Finally, the best-studied groups of mycoparasites

Fig. 3. Phylogenetic tree showing main ecological transitions across the Dikarya fungi. Symbols on the right indicate that the transition has occurred within the group.
lie within the Pezizomycotina, with representatives within the Sordariomycetes (Goh & Vujanovic, 2010; Vujanovic & Kim, 2017) and particularly in the Hypocreales (Inglis & Kawchuk, 2002; Atanasova et al., 2013; Quandt, Bushley & Spatafora, 2015), Dothideomycetes, Eurotiomycetes and Orbiliomycetes (Tzean & Estey, 1976; Jeffries, 1995), as well as in the genera Pyxidiophora (Laboulleniomyces) (Blackwell, 1994; Kirchner, 2003; Goldmann & Weir, 2018) and Teratosperma (Pezizomycotina incertae sedis) (Parfitt, Coley-Smith & Jeves, 1983) (Fig. 3). Equally diverse are their hosts, which even include Oomycetes (Jeffries, 1995; Inglis & Kawchuk, 2002). Infected fungi can defend themselves from such attacks by producing toxic secondary metabolites, melanin, and reactive oxygen species (Zeng et al., 2014; Chamoun, Aliferis & Jabaji, 2015; Karlsson et al., 2015), as well as by inducing cell death (Druzhinina et al., 2011). Fungi can infect plants, algae and other fungi in biotrophic, parasitoid or necrotrophic interactions. Necrotrophic mycoparasites can be highly aggressive and often have a broad range of hosts (Jeffries, 1995; Atanasova, Jensen & Zeilinger, 2017). Some of these seem to be able to colonize plant tissues as endophytes (Fig. 4), where they provide an effective defence mechanism against fungal pathogens for the host. Such properties have raised considerable interest in the use of mycoparasites as agricultural pest-control agents, including the prospect of preventive treatments by inducing colonization of desired endophytes. This has driven much research in this fungal niche. *Trichoderma* has notable expansions of the chitinase genes, as well as a diverse pool of secondary metabolism enzymes (Druzhinina et al., 2011; Kubicek et al., 2011; Mukherjee et al., 2013; Atanasova, Jensen & Zeilinger, 2017). However, experimental evidence suggests that the functional specialization of these enzymes is limited (Gruber & Seidl-Seiboth, 2012) and trophic strategies are variable even within the genus (Atanasova et al., 2013). Other important mycoparasites in the Hypocreales, for which genomic information is available, are the genera *Tolysiphonium* (Quandt, Bushley & Spatafora, 2015), *Clonostachys* (Karlsson et al., 2015) and *Escovopsis* (de Man et al., 2016). Genome comparisons of these mycoparasites show that mycopathism has evolved independently and through different strategies (Fig. 4). Biotrophic parasites are experimentally less tractable and they produce less-severe symptoms on a narrower range of hosts. Despite this, *Amphelomyces* (Park et al., 2010; Pintye et al., 2012, 2015) and related genera in the Pleosporales have been studied as possible biocontrol agents against powdery mildews, although in this case their host range is unusually broad (Sullivan & White, 2000; Park et al., 2010; Pintye et al., 2012, 2015). Genomic data from this group of mycoparasites is limited, but transcriptomic data show that pathogenesis depends on the secretion of uncharacterized toxins and a wide array of extracellular proteases (Siozios et al., 2015). Interestingly, transcripts from many of the genes upregulated during infection are also stored in resting spores of *Amphelomyces*. Finally, due to their evolutionary position, several mycoparasitic members of the Zoopagomycota (*Dimargaris* in the Kickxellomycotina; *Piptocephalis*, *Syncephalis* and *Thamnocephalis* in the Zoopagomycotina) are being sequenced as part of the 1000 fungal genomes consortium initiative.

From an evolutionary standpoint, there seems to be a relationship between mycoparasites and pathogens of invertebrates (Druzhinina et al., 2011) (Fig. 4). For instance, the blastoclad *Catenaria* (James, Porter & Martin, 2014), the Orbiliomycetes *Arthrobotrys* (Tzean & Estey, 1976) and the Hypocreales *Trichoderma* and *Clonostachys* (Li et al., 2015), have been reported as both mycoparasites and nematode parasites. Mycoparasites might show other lifestyles as well. For instance, it has been reported that mycoparasitic *Trichoderma* species can act as plant pathogens, combining the two approaches to bulldozing through mycorrhizae as a mean to invade plant tissue (De Jaeger, Declerck & De La Providencia, 2010). It is important to note that several important characteristics for a mycoparasite are commonly or necessarily found in nearly all saprotrophs. To attack other fungi they require chitin-degrading enzymes; which they must have if they possess a chitinous cell wall. Mycoparasites must also protect themselves from enzymatic degradation (Gruber & Seidl-Seiboth, 2012), Production of toxic compounds is an effective, and very common strategy used to defend a territory, but can also be easily applied for offensive purposes. The formation of penetrating structures (haustoria) is common in many mycoparasites, although similar structures are common in parasites of all kind of hosts and thus the presence of haustoria does not imply any degree of specialization. Mycoparasites could serve as donors and facilitators for horizontal gene transfer (HGT), by either donating DNA directly to the host or by removing the host cell wall, thereby eliminating the main physical barrier for the acquisition of DNA from other species. Gene transfer from *Parastella* (Mucorales) to its host, *Absidia* (Mucorales) has been shown to take place in laboratory conditions (Kellner et al., 1993). A wide range of mycoparasites might theoretically even acquire genes from a host and subsequently donate them to another, effectively acting as vectors. More importantly, since many of these broad-spectrum parasites are saprotrophic filamentous fungi, just like their hosts, ecological barriers are probably smaller than for other parasitic vector systems. In any case, it is important to note that our knowledge on mycoparasitic interactions remains very limited. Such interactions are usually described either during a search for pest-control agents or by sporadic findings during environmental fungal biodiversity surveys. Because of this, the scope and ecological relevance of mycoparasites cannot yet be accurately estimated. For instance, just like the case of *Arthrobotrys*, many well-known fungi might be facultative mycoparasites only under the right conditions. Undoubtedly, we have barely scratched the surface of this topic.

(2) **Fungi and protozoans**

The relationship between fungi and amoeboid protozoans is largely unexplored. Both groups of organisms are
Evolutionary and ecological transitions in fungi

Fig. 4. Schematic representation of known relationships between fungal ecotypes. Each connecting arrow can be uni- or bidirectional. Each pathway illustrates an example of a group that has undergone such a transition; in most cases there are other known cases in which the transition has occurred. For the endolichenic to endophyte transition, environmental clades without a formal taxonomical description were described by U'Ren et al. (2010).
common inhabitants of soils and they have frequent ecological interactions. Amoeboid protozoans are able to predate fungi, and probably are important in the control of fungal biomass. Mechanisms to prevent, survive or escape phagocytosis have been described for certain human pathogens (e.g. Candida, Cryptococcus) where this trait is useful for evading the host immune system, such as engulfment by macrophages (Mylonakis, Casadevall & Ausubel, 2007; Jiménez-Guri et al., 2013; Paes et al., 2013). Some of these strategies are sophisticated, and have been proposed to represent exaptation of traits evolved under the pressure of phagotrophic protozoans (Collette & Lorenz, 2011; Jiménez-López & Lorenz, 2013; Seider et al., 2014). Some groups of protists can predate fungal mycelia and spores, and seem to be important factors controlling fungal populations (Adl & Gupta, 2006).

The opposite situation, with fungi feeding on amoebae, has been described for several groups (Corsaro et al., 2017). Amoebophagous fungi typically follow two types of strategies: endoparasitism and trapping. In endoparasitism the fungi enters the cell, usually as a spore, to then develop a thallus inside the host. This has been described in Rozellidea (Nucleophaga, Paramicrosporidium) and Zoopagomycotina (family Cochlonemataceae) (Fig. 1). On the other hand, amoeba-trapping fungi produce structures, which can be as simple as the spore, that attach to the amoeba and produce a mycelium that penetrates the microorganism to feed on its cytoplasmic content. This strategy is known in the Zoopagomycotina (family Zoopagaceae) (Duddington, 1956; Benny, Humber & Voigt, 2014; Corsaro et al., 2017), the Pezizomycotina (Class Orbiliomycetes) (Duddington, 1956; Pfister, 2015; Corsaro et al., 2017), and the Agaricomycetes (McLaughlin & Spatafora, 2014; Quandt et al., 2017) (Figs 1 and 3).

The first batch of amoebophagous fungal genomes was published at the beginning of 2019, all from the Zoopagomycotina, although the samples represent metagenomes due to the difficulty of separating them from their hosts (Davis et al., 2019). The limited number of described taxa that infect amoebae is certainly misleading. Studies of amoebae in general are surprisingly neglected, even more so with regard to their parasites. The biomass of such fungi in natural environments is very low, and even when detected by molecular methods, it is normally very difficult to associate a sequence with its ecological niche. Furthermore, the Zoopagomycotina, which contain most currently described species of amoebophagous fungi, possess abnormally long internal transcribed spacer (ITS) regions, hindering their detection in typical environmental barcoding studies. Here we shall argue that this gap in knowledge is limiting our understanding of the fungi in key areas. First, the relationship between Rozellidea and Microsporidia and the evolutionary origin of the latter requires the description of more members of Rozellidea, a task that has advanced in recent years due to research on amoebal parasites (Corsaro et al., 2014a, 2014b, 2016). Second, all groups of amoeba-trapping fungi also contain nematode-trapping species (Duddington, 1956; Corsaro et al., 2017) (Fig. 4). Traps for amoebae are normally much smaller and simpler, and one can hypothesize that invertebrate traps evolved from ancestral amoebal trappers. On the other hand, it is also possible that amoebae-trapping fungi descend from nematophagous fungi, after simplification of their trapping structures. The latter scenario has been proposed recently for the Zoopagomycotina (Corsaro et al., 2017), while other authors prefer the former hypothesis (Davis et al., 2019). This debate is particularly interesting in the context of the Orbiliomycetes, since this class is the earliest-diverging lineage within the hyperdiverse Pezizomycotina. Finally, it is widely acknowledged that fungi must have been one of the earliest lineages of eukaryotes to populate emerged land (Taylor & Osborn, 1996; Knoll, 2014), pre-dating land plants and terrestrial arthropods. There is, however, very little reason not to assume that amoebae thrived in these early land ecosystems. In fact, the earliest radiation of terrestrial fungi (Zoopagomycota) is traditionally associated with invertebrate parasitism, and the role that amoebae had in the ancestral diversification of these organisms should be seriously considered.

V. FUNGI AND ANIMALS

(1) Overview

Fungal biomass is abundant in the environment and has a high nutritional value for metazoans. Compared to cellulose provided by plants, chitin is easier to digest and contains a higher nitrogen content. These characteristics make microscopic fungi an important food source for soil invertebrates such as Arthropoda, Annelida, Mollusca or Nematoda (Johnson et al., 2005; Crowther, Boddy & Jones, 2011a, 2011b; Crowther, Boddy & Hefin, 2012). Some species of termites, ants or beetles (Mueller & Gerardo, 2002; Mueller et al., 2005; Schuelke et al., 2017), as well as certain snails (Stillman & Newell, 2003), are known to culture fungal biomass and use it as a primary food source. Many macroscopic fruiting bodies and lichen thalli are edible and constitute an important food source for animals, including humans (de Mattos-Shipley et al., 2016).

Many fungal lineages are tightly associated with animals (Figs 1 and 3). Most studies have focused on fungal parasites of vertebrates, insects or nematodes, but fungal pathogens are known for at least anecdotal cases in Mollusca (Van Dover et al., 2007), Annelida (Vakili, 1993), Rotifera (Barron, 1980), Tardigrada (Drechsler, 1951), Platyhelminthes (Mikhailov, Simdyanov & Aleoshin, 2017) and Cnidaria (Fisher et al., 2012; Toledo-Hernández et al., 2013). For the sake of simplification we do not make a distinction between a parasite, pathogen or even a predatory fungus in this section. Obligate parasites require the host to complete their life cycle and usually are tightly associated with the internal tissues or surface of their host. Facultative parasites might use
Evolutionary and ecological transitions in fungi

2014; Nishino

many of which prey on nematodes and other soil microfauna, often in response to nutrient limitation (Meerupati et al., 2013; Liu et al., 2014; Nishino et al., 2016; Gomez-Polo et al., 2017; Jiang, Xiang & Liu, 2017). Many species are opportunistic pathogens, infecting animals only occasionally and normally only when host immunity is weakened. Animal parasitism has evolved independently many times, and it is noteworthy that several very ancient lineages contain highly specialized animal parasites. Finally, many fungi live in association with metazoan tissues without causing any apparent harm, a relationship often called commensalism. Despite the great animal diversity that exists in nature, the immune response to fungi is very similar in virtually all groups, primarily relying on phagotrophic immune cells and the production of extracellular traps (Mylonakis, Casadevall & Ausubel, 2007; Branzk et al., 2014; Zhang & Soldati, 2016). Finally, there are some reports of symbiotic fungi associated with animals. In most cases, these symbionts are unculturable, and thus very little is known about their physiology or even taxonomic affiliation. In this regard, several species of Cicadidae, Cicadellidae and Coccidae (Hemiptera) have lost their traditional bacterial symbionts and have substituted them with a fungal partner affiliated with the entomopathogenic genus Ophiocordyceps (Sordariomycetes) (Nishino et al., 2016; Gomez-Polo et al., 2017; Matsuura et al., 2018). It is very likely that Ophiocordyceps evolved several times independently as a symbiont (Fig. 4), and we are certain that future studies will reveal the underlying genomic changes that govern this peculiar transition.

(2) Obligate parasites of animals

Obligate fungal parasites of metazoans present hallmarks of genomic and metabolic reduction, typical of highly specialized parasites. Here, we review genomic information regarding various important lineages of obligate parasites: Microsporidia, Zoopagomycota, the genus Pneumocystis (Taphrinomycotina), the poorly studied Laboulbeniomycetes (Pezizomycotina) and the Septobasidiales (Pucciniomycotina) (Figs 1 and 3). We also include in this category the Nephridiophagida, for which no genomic information is currently available.

Microsporidian parasites are known for many metazoan lineages, including several marine taxa. Microsporidia are characterized by an extreme genome reduction, loss of many essential metabolic pathways and the presence of mitochondria-derived mitosomes (Peyretaillade et al., 2011; Corradi & Selman, 2013). Their sister group, the Rozellida, has been shown to contain species with a microsporidia-like intracellular lifestyle that parasitize amoebae (Corsaro et al., 2014b,a, 2016). Based on this, it is likely that Microsporidia were already parasites of unicellular ancestors of metazoans. This hypothesis implies two main predictions. First, microsporidian parasites of non-metazoan Holozoa should exist. Second, the phylogenetic position of these hypothetical microsporidia within the context of the whole group should be early branching. In agreement with this hypothesis, microsporidian parasites of marine invertebrates seem to be more ancient (Corradi & Selman, 2013; Mikhailov, Simdyanov & Aleoshin, 2017), although the diversity of such organisms is still poorly explored and their phylogenetic position remains uncertain. Alternatively, Microsporida might have jumped to metazoans from protozoans. Metchnikovellidae are known to be able to infect gregarines, an important group of animal parasites, and free-living ciliates (Bass et al., 2018). Since Metchnikovellidae are one of the earliest splitting lineages of Microsporida, this is a very plausible scenario.

Zoopagomycota also comprises many obligate parasites of metazoans, especially of insects in the Entomophthoromycotina and of nematodes in the Zoopagomycotina. It is noteworthy that this is the earliest-diverging clade of terrestrial fungi. For Entomophthoromycotina, ancestral character reconstruction analyses have suggested that they all descend from filamentous saprotrophs that could facultatively infect insects, similar to Conidiobolus species (Gryganskiy et al., 2013) (Fig. 4). Given that traditional filamentous growth and saprotrophy can also be found in Kickxellomyctina and considering the basal position of Entomophthoromycotina within Zoopagomycota, we shall argue that it is valid to extrapolate those results to the whole phylum. Despite this, it is very likely that animal parasitism evolved independently and through different means in the three lineages. The earliest diverging Entomophthoromycotina appear to be associated with arthropod exuviae and corpses (Manning, Waters & Callaghan, 2007; Manning & Callaghan, 2008), and probably evolved first as specialized saprotrophs before shifting to obligate parasitism (Gryganskiy et al., 2012, 2013) (Fig. 4). Zoopagomycotina contains some obligate nematode-trapping parasites, although most species of the group infect either other fungi or amoebae. Recent phylogenetic analyses suggest that nematode and rotifer parasite lineages are basal within the group, suggesting that they might represent the ancestral lifestyle (Corsaro et al., 2017). Harpellales, an order within the Kickxellomyctina, also contains insect parasitic species (e.g. some Smittium species), but in these cases parasitism seems to have evolved secondarily from commensals (Manning, Waters & Callaghan, 2007; Manning & Callaghan, 2008). Genome sequencing revealed that Harpellales have a highly variable genome size, from 28.7 Mbp in Zancudomyces culisetae to 102.4 Mbp in Smittium mucronatum (Corsaro et al., 2017). Proteome size varied from 8000 to 12500 predicted protein-coding genes in the four sequenced species in that study. All these parameters are within the range of typical free-living fungi. To date, only one draft genome of an obligate parasite in the Entomophthorales, Entomophthora muscae, is available in GeneBank. The genome size for this species is around 24 Mbp, which is small for most fungi, but not unusually so. Finally, a high evolutionary rate, a typical result of obligate parasitism, is known in Zoopagomycotina (Tanabe et al., 2000).
The genus *Pneumocystis* (Taphrinomycotina) contains several highly specialized lung parasites of mammals, including humans. The genome of this parasite shows clear signs of genome reduction, particularly of most genes in the biosynthetic pathways of several amino acids, sterols, myo-inositol and even cell wall components (Hauser et al., 2010; Porollo et al., 2014; Ma et al., 2016). No other genera of the Pneumocystidomycetes are known, and *Pneumocystis* is the only animal-associated member of the Taphrinomycotina, making it currently impossible to infer how this parasitic genus evolved from non-parasitic relatives.

Laboulbeniomycetes is a peculiar class within the Pezizomycota that that use specialized haustoria to latch onto the cuticle of insects, mites and some Diplopoda, usually to the antennae or mouthparts (Haelewaters et al., 2015). The inclusion in Laboulbeniomycetes of the genus *Pyxiidiophora*, which has been described as a mycoparasite, implies that its insect-associated lifestyle probably evolved from a fungus-associated ancestor (Blackwell, 1994; Kirschner, 2003) (Fig. 4). Unfortunately, genomic information on this group is very limited, mostly due to the experimental limitations caused by their peculiar lifecycle (Haelewaters et al., 2015; Goldmann & Weir, 2018). Finally, the genera *Septobasidium* and *Urediniella* (Septobasidiales; Pucciniomycotina) comprise several species of obligate parasite of scale insects (Henk & Vilgalys, 2007; Araújo & Hughes, 2016). The 1000 fungal genomes project includes a few species of Laboulbeniomycetes planned for genome sequencing; while the genome of *Septobasidium* appears complete and pending publication.

(3) Facultative parasites of animals

Many free-living fungi are able to infect different groups of animals (Figs 1 and 3). These parasitic relationships are often very specific, in a manner similar to that of necrotrophic plant pathogens. In host-specific parasites the fungus might display highly sophisticated pathogenic mechanisms that include, but are not limited to: immune evasion, toxins, secretion of hydrolytic enzymes for structural components, or even the ability to induce behavioural changes in the host. Unlike obligate parasites, which tend to limit harm to the host and are dependent on host demography, facultative pathogens often cause high morbidity, and are largely independent of host population density (Fisher et al., 2012). This in turn might lead to some of these pathogens causing great damage to natural host populations and, in some cases, leading to extinctions. For example, *Aspergillus sydowii* has caused great damage to coral reefs, in an opportunistic infection that has become widespread as a result of global warming (Tanabe et al., 2000; Toledo-Hernández et al., 2013). The specificity and independence of some of these parasites make them very attractive as pest-control agents, specially against nematodes and insects. Finally, some of these fungi are able to infect mammals, including humans (Hauser et al., 2010; Porollo et al., 2014; Ma et al., 2016). Human mycoses range from mildly unpleasant dermatological infections to life-threatening colonization of internal organs. Far from anecdotal, the health cost of these infections is very high, despite being historically neglected by medical communities and mostly unknown by the general public (Brown et al., 2012).

Arthropods are by far the most diverse animal phylum in terrestrial environments where fungi abound. Arthropod mycoses caused by zoosporic fungi and Basidiomycota are known, but they are rather uncommon (Gleason et al., 2010; Araújo & Hughes, 2016) (Figs 1 and 3). Here we highlight the genus *Fibularhiszosticta* (Atheliales, Agaricomycetes), that mimics termite eggs in order to infiltrate their nests (Matsuura, 2006; Yashiro & Matsuura, 2007; Matsuura et al., 2009; Araújo & Hughes, 2016). As mentioned above, virtually all members of the Entomophthoromycota are able to parasitize insects to some degree. *Conidiodobolus* and *Basidiobolus* are among the only members of the clade that are not obligate parasites. These two genera are apparently associated with arthropod exuviae, and are able to use their chitin-degrading capabilities to occasionally infect living insects (Manning, Waters & Callaghan, 2007; Manning & Callaghan, 2008). Only one species of Mucoromycotina, *Spordiniella undella* (Mucorales), is described as a facultative entomopathogen (Evans & Samson, 1977; Araújo & Hughes, 2016). Insect parasites have evolved several times independently within the Pezizomycotina [orders Pleosporales (*Podonectria*), Myriangiales (*Myriangium*), Ascosphaerales (*Ascosphaera*), and Hypocreales] (Araújo & Hughes, 2016; Dao et al., 2016), and they are particularly diverse within the Hypocreales (Boomsma et al., 2014; Araújo & Hughes, 2016) (Fig. 3). Some of these Hypocreales (e.g. *Cordyceps*, *Beauveria*, *Ophiocordyceps*) are highly host specific, and some species have the ability to influence host nervous system and modify host behaviour to aid spreading their spores (Araújo & Hughes, 2016; Butt et al., 2016; Shang et al., 2016; Wang & Wang, 2017). Insects, on the other hand, can defend themselves using macrophages, antimicrobial peptides, melanin and reactive oxygen species, as well as adopting certain behaviours, such as eliminating infected members of a colony or exposing themselves to higher temperatures (Dubovskiy et al., 2013; Ortiz-Urquiza & Keyhani, 2015; Lu & St. Leger, 2016; Wang & Wang, 2017). Entomopathogenic Hypocreales descend from either endophytes or plant pathogens (Boomsma et al., 2014; Wang & Wang, 2017) (Fig. 4). More importantly, endophytic Hypocreales are known to produce toxins that protect plants against herbivory and other fungi, which probably represents an intermediate stage towards the evolution of entomopathogenicity (Porras-Alfaro & Bayman, 2011; Boomsma et al., 2014; Hardoim et al., 2015). In virtually all cases described above, the fungus is able to grow on the insect body after killing it, and very likely exists as a more or less active mycelium in the environment independently from the host. It is important to note that arthropod parasites must be able to use trehalose as a carbon source, a molecule that is highly abundant in the tissues of these animals.

Microinvertebrates are an important fraction of the biomass in soils, sediments and other environments, and
several groups of fungi have acquired the ability to infect them (Figs 1 and 3). Nematodes are the best-studied fraction of this community of microinvertebrates, due to their relevance to agricultural productivity, and nematophagous fungi have been studied for their potential as control agents. Nematode parasites can be found in the Zoopagomycotina (Duddington, 1956; Benny, Humber & Voigt, 2014), Sordariomycetes, Orbiliomycetes, Eurotiomycetes (Pezizomycotina) (Jiang, Xiang & Liu, 2017), Agaricomycetes (Agaricomycotina) (Duddington, 1956; de Mattos-Shipley et al., 2016), Mortierellomycotina (Jiang et al., 2011), Entomophtheromycotina (Saikawa, Oguchi & Ruiz, 1997), and even in the Blastocladiomycota (Gleason et al., 2010; Singh et al., 2012, 2013). Many nematophagous fungi behave like regular filamentous saprotrophs, but are prone to attack eggs and other resting structures, such as non-motile females in certain groups of plant parasitic nematodes (Chen, Dickson & Mitchell, 1996; Olivares & López-Llorca, 2002; Eappen, Beena & Ramana, 2005; Sun et al., 2006; De et al., 2008). Nematophagous Agaricomycetes, such as Coprinus or the oyster mushroom Pleurotus, produce paralyzing toxins that allow for consumption of even mobile life stages (de Mattos-Shipley et al., 2016). Many of these fungi produce specialized structures that can cause mechanical damage or contain toxins and mucilaginous traps. The terminology of such structures is highly variable: ‘spiny balls’ in Coprinus (Luo et al., 2004, 2007), stephanocysts in Hyphoderma (Bursdal, 1969; Hallenberg, 1990), acanthocytes in Stropharia (Luo et al., 2006), or appendages in Nematoclonus, Conocybe and Pleurotus (Dreschler, 1941, 1946, 1949, 1954; Luo et al., 2007). There is currently little information regarding the homology or even the distribution of such structures among Agaricomycetes. Some nematophagous fungi, specially within the class Orbiliomycetes, are well known for the production of highly elaborate traps, for which several morphologies exist and that have granted them the alias of ‘carnivorous fungi’ (Duddington, 1956; Yang et al., 2012; Jiang, Xiang & Liu, 2017; Su et al., 2017; Vidal-Diez de Ulzurrun & Hsueh, 2018). The last strategy consists of the production of spores that are then ingested by the worm or stick to it. The spore germinates and the mycelium invades and consumes the nematode. The genomes of several nematophagous fungi are available (Yang et al., 2011; Lai et al., 2014; Larriba et al., 2014; Liu et al., 2014; Zhang et al., 2016), and analyses have shown that they tend to contain gene expansions in families of chitin-degrading enzymes and proteases. Furthermore, nematode-trappers tend to possess a well-developed cellulose-degrading metabolism, but few traditional plant pathogenesis-related genes, suggesting saprotrophic ancestry (Liu et al., 2014) (Fig. 4). These adaptations are very similar to those found in entomopathogenic and mycoparasitic fungi, and interconversion between these different lifestyles seems to have been common in the Hypocreales (Pezizomycotina) (Zhang et al., 2016). Many nematophagous fungi are known to associate with plants as endophytes or wood decomposers (Luo et al., 2004; Larriba et al., 2014; Wani et al., 2015; de Mattos-Shipley et al., 2016) (Fig. 4). Again, the endophytic lifestyle is very common among nematophagous, entomopathogenic and mycoparasitic Hypocreales, and these capabilities might have evolved as part of a symbiotic relationship in which the fungus protects the plant against parasites (Fig. 4).

Separating vertebrate parasites within this review goes beyond a simple anthropocentric point of view, since vertebrates present several important peculiarities when compared to other animal groups. First of all, vertebrates have large sizes and entail a considerable diversity of body micromeres. Second, they lack chitin structures. Third, they all possess a well-developed antibody-based immune system, which imposes a serious challenge to any microbe trying to grow inside them. A subset of vertebrates (birds and mammals) are warm-blooded organisms whose internal temperature imposes yet another important barrier for microbes (Casadevall, 2012). Fungi are an important concern for conservation, and three particular cases illustrate this. Batrachochytrium dendrobatidis (Longcore, Pessier & Nichols, 1999; Berger et al., 2005; Fisher, Garner & Walker, 2009; Joneson et al., 2011; Voyles, Rosenblum & Berger, 2011; Byrne et al., 2016) and B. salamandridivorans (Gray et al., 2015; Yap et al., 2017) are two related chytrid species that cause fatal skin damage to amphibians and are threatening populations globally. The second most important menace to vertebrates is the dothideomycete Pseudogymnoascus destructans, that is causing massive bat mortality in North America (Foley et al., 2011; Fenton, 2012; Cryan et al., 2013; Alves, Terrible & Brito, 2014; Leopardi, Blake & Puechmaillle, 2015). This highly virulent strain arrived from Europe, where the native bat populations are resistant to it (Leopardi, Blake & Puechmaillle, 2015). The fungus is actually psychrophilic, and colonizes soft tissues of bats while they are hibernating and their body temperature drops. Fusarium solani is a fungus that is causing great harm to sea turtles, as it colonizes and destroys the eggs of these reptiles (Sarmiento-Ramirez et al., 2010, 2014). This is a particularly interesting case since Fusarium is a traditional plant-pathogenic genus (Gauthier & Keller, 2013) (Fig. 4).

Fungal infections in humans are a cause of great public health concern (Warnock, 2007; Ostrosky-zeichner, 2012; Kim, 2016; Vallabhaneni et al., 2016). The most common fungal infections are dermatological and rarely life threatening, but can cause considerable discomfort and aesthetic problems, and can be very difficult to treat (Revankar & Sutton, 2010; Teixera De Aguiar Peres et al., 2010; Ricardo Criado et al., 2011; Achterman & White, 2013; Cafarchia et al., 2013; Chowdhary, Perfect & de Hoog, 2014; Seyedsoudavi et al., 2014; White et al., 2014). Most fungi causing dermatological infections are members of the black fungi [orders Pleosporales (Dothideomycetes) and Chaetothyriales (Eurotiomycetes)]. These fungi have evolved to colonize highly hydrophobic and irradiated environments, which can be similarly represented by a desert rock or a human nail (Cafarchia et al., 2013) (Fig. 4). Unrelated to these but also causing skin infections are members of the genus Malassezia (Ustilaginomycotina) (Xu et al., 2007; White et al., 2014;
Velegraki et al., 2015). Beyond these, some members of the Onygenales, an order of black-fungus-related organisms specialized in degrading keratinized tissues, have acquired the ability to grow in skin and other body environments, particularly in lungs. The main pathogens are members of the genera Histoplasma (Malcolm & Chin-Hong, 2013; Garfoot, Zemska & Rappleye, 2014; Horwath, Fecher & Depepe, 2015), Blastomyces (Saccenate & Woods, 2010; Bariola & Vyas, 2011; López-Martínez & Méndez-Tovar, 2012; Malcolm & Chin-Hong, 2013; Castillo, Kauffman & Miceli, 2016), Coccioidioides (Nefsey et al., 2010; Malcolm & Chin-Hong, 2013; Whiston & Taylor, 2014) and Paracoccidioides (Malcolm & Chin-Hong, 2013; de Oliveira et al., 2015; Gonzalez & Hernandez, 2016). Fungi in these genera are highly melanized, which allows them to survive highly oxidative conditions such as those resulting from macrophage attack, and specialized adaptations to intraphagosomal growth have been described (Garfoot, Zemska & Rappleye, 2014). The second most-common group of human pathogens are members of the Saccharomycotina (Bennett, 2009; Butler et al., 2009; Arendrup, 2013; Modrzewska & Kurnatowski, 2013; Holland et al., 2014; Glöckner & Cornely, 2015; Priest & Lorenz, 2015; Gabaldón, Naranjo-Ortiz & Marcet-Houben, 2016), particularly yeasts from the genera Candida and Nakaseomyces that cause both superficial infections in mucosae and systemic bloodstream infections with high mortality. The group include highly specialized human commensals, such as Candida albicans and Nakaseomyces glabratus (syn. Candida glabrata), and opportunistic pathogens that arrive on the host from the environment. Several yeast species have adaptations to face phagocytosis, as well as the ability to form biofilms together with bacteria (Modrzewska & Kurnatowski, 2013; Holland et al., 2014; Glöckner & Cornely, 2015; Priest & Lorenz, 2015). Cryptococcus is a yeast-like member of the Tremellomycetes that causes pneumonia and meningitis (Chaturvedi & Chaturvedi, 2011; Kwon-Chung et al., 2014; Srikanta, Santiago-Tirado & Doering, 2014; Dylag, 2015; Herbert et al., 2017). The fungus presents a mutinucleated and highly polyloid titan cell that seems to avoid phagocytosis thanks to its sheer size, and from which apparently regular-sized cells emerge and colonize. The genus Cryptococcus has a dual life as a filamentous mycoparasite (Filobasidiella), and thus human parasitism is a derived state (Kwon-Chung, 1975, 1976; Ginns & Malloch, 2003; Rodriguez-Carres et al., 2010). Finally, other filamentous fungi in the Pezizomycota (Aspergillus, Penicillium, Paecilomyces, Ascomycota, Fusarium, Trichoderma, Sporothrix, Scedosporium), Pucciniomycota (Rhodotorula), Mucoromycota (Rhizopus, Lichtheimia, Mucor) and Entomophthoromycotina (Basidiobolus, Conidiobolus) produce opportunistic and highly invasive infections in soft tissues (Groll & Walsh, 2001; Fleming, Walsh & Anaissie, 2002; Enoch, Ludlam & Brown, 2006; Cornely, 2008; Richardson & Lass-Florl, 2008; Miceli & Lee, 2011; Shoham, 2013; Crabol & Lortholary, 2014). These fungi are usually air- and soil-borne saprotophs that can grow rapidly, without being excessively inhibited by high temperature (Fig. 4). The course of these diseases is very variable. Some produce nodules that can cause organ damage or, at least, severe disfiguration. Others develop as chronic infections that cause sustained damage to organs. Pulmonary aspergillosis is the most common of these diseases, causing a wide range of respiratory problems (Tekaia & Latgé, 2005; Fedorova et al., 2008; Kousha, Tadi & Soubani, 2011; Kosmidis & Denning, 2015; Hayes & Novak-Frazer, 2016). Finally, some of these fungi are highly virulent and grow rapidly through soft tissues, which can lead to severe mutilation and organ damage. Great efforts have been dedicated to understanding how opportunistic pathogens emerge. While the mechanisms are highly variable, often pathogens display gene expansions in certain strategic protein families (e.g. cell adhesion, proteases, lipidas, scavenging of reactive oxygen species). Many human fungal pathogens seem to have highly heterozygous and even unstable genomes, with common aneuploidies, polyploidies (Cottier & Pavelka, 2012; Forche, 2012; Li et al., 2012; Morrow & Fraser, 2013; Bennett, Forche & Berman, 2014) and hybridization events (Cottier & Pavelka, 2012; Forche, 2012; Li et al., 2012; Morrow & Fraser, 2013; Bennett, Forche & Berman, 2014; Heitman et al., 2014; Short, O’Donnell & Geiser, 2014; Pryszcz et al., 2015; Mixão & Gabaldón, 2018). It is entirely possible that these events are also common in other fungi. Nevertheless, aneuploidies have been linked to acquisition of antifungal resistance and hybridization has been related to the emergence of new virulent strains in certain species complexes (Mixão & Gabaldón, 2018).

(4) Fungal commensals of animals

Some lineages of fungi are commonly or even exclusively found in non-harmful association with animal surfaces, both internal and external (Figs 1 and 3). Some lineages within the Kickxellomycotina live in association with the gut of aquatic insect larvae (Harpellales), isopods and springtails (Asellariales) (Benny, Humber & Voigt, 2014; Tretter et al., 2014). These fungi possess very small thalli and cannot be cultured in the laboratory without their hosts, which makes them extremely difficult to study.

Yeasts in the Saccharomycotina are common components of the gut microbiota in insects (Kurtzman & Sugiyama, 2015; Blackwell, 2017; Kijpornspongpan et al., 2019), as well as in vertebrate mucosae (Iliev & Underhill, 2013; Wang et al., 2014d; Limon, Skalski & Underhill, 2017). It has even been proposed that the insect gut might have been an important environment for the evolution of Saccharomycotina (Blackwell, 2017) (Fig. 4), and some genera, such as the recently described Subomyces (syn. Saccharomycyes tanzawaensis) seem to be found preferentially in such niches (Kijpornspongpan et al., 2019). Insects feeding on sap or fruits have diets that are extremely rich in simple sugars. Members of the Symbiotaphrinales (Xylonomycetes) have been described in association with several groups of beetles (Noda & Kodama, 1996; Baral et al., 2018), where they seem to help their host to detoxify plant toxic compounds (Shen & Dowd, 1989, 1991). Beyond that, some species are common members of healthy vertebrate mucosae. Due to
its relevance as a human pathogen, *Candida albicans* has been extensively studied. In addition to this, other yeast-like forms in Basidiomycetes are important commensals of mammalian skin and mucosae.

An important and often-overlooked community of fungal vertebrate commensals are the members of Neocallimastigomycota (Kittelmann et al., 2012; Gruninger et al., 2014). Virtually no study has tackled the question of how these singular fungi interact with the host immune system. Neocallimastigomycota represent an evolutionary conundrum. As one of the earliest-diverging lineages of fungi, they must have diverged much earlier than the appearance of their current vertebrate hosts. This implies one of three scenarios. The first possibility is that these fungi developed their signature lifestyle very recently, by associating with their vertebrate hosts. The second possibility is that these fungi evolved in association with other, probably extinct lineages. For instance, it is assumed that large herbivorous dinosaurs probably had a fermentative digestion in which a role for Neocallimastigomycota is very likely (Clauss et al., 2013). There is a report of morphological identification of Neocallimastigomycota in the gut of a sea urchin (Thorsen, 1999), which raises the possibility that these fungi might also associate with marine animals. Finally, members of this lineage might live in yet unexplored environments, from which they could have arrived to the vertebrate host and established as important commensals.

VI. THE FUNGUS–PLANT BIOME: ECOLOGICAL INTERACTIONS BETWEEN PLANTS AND FUNGI

(1) Overview

Fungi and land plants share one of the longest running, most-intimate relationships in the biosphere (Figs 1 and 3). Fungi have lived in association with plants probably since long before they started growing on land (Lücking et al., 2009; Krings, Taylor & Dotzler, 2013; Strullu-Derrien et al., 2014; Delaux et al., 2015; Morris et al., 2018). The fungal kingdom is responsible for a large proportion of plant diseases, and they are also the main decomposers of plant necromass. On the other hand, plants have myriad fungi in tight association with their tissues in the form of symbionts and/or commensals. Mycorrhizae are symbiotic fungi associated with the roots that help the plant to obtain nutrients and water. Endomycorrhizal associations exist for approximately 90% of plant species (Tedescoo, May & Smith, 2010; Davison et al., 2015). In addition, endophytes are fungal commensal associates that live inside plant tissues without causing harm to the plant (Faeth & Fagan, 2002; Rodriguez et al., 2009; Sun & Guo, 2012; Strobel, 2014; Hardoin et al., 2015). The definition varies among authors, and some even include asymptomatic pathogens and mycorrhizal fungi. Endophytes have not enjoyed the spotlight to the same extent as mycorrhizae, and thus precise estimations of their abundance, relevance and diversity are still lacking. The presence of these fungi seems to protect the plant against pathogenic fungi, by stimulating plant defences and by acting as a niche competitor (Rodriguez et al., 2009; Hardoin et al., 2015; Wani et al., 2015). Some of these fungi are parasites of other organisms, such as other fungi, insects or nematodes, produce secondary metabolites that help the plant against herbivores, or promote plant growth (Vega et al., 2008; Rodriguez et al., 2009; Hardoin et al., 2015; Wani et al., 2015). Even less studied are fungi living on the surface of the plants themselves (epiphytes), which form the so-called phyllosphere communities (Porras-Alfaro & Bayman, 2011; Kempel & Mueller, 2014; Vacher et al., 2016; Datlof et al., 2017). These communities are highly diverse and, like endophytes, can affect the physiology of their host plants. They represent an unexplored pool of biological diversity that is very often overlooked during conservation efforts (Blackwell & Vega, 2018).

(2) Mycorrhizae and plant commensal associates

Mycorrhizal associations appear in Glomeromycota, Mucoromycota (Endogonales), Agaricomycetes and several classes of Ascomycota (Schüssler, Schwarzott & Walker, 2001; Tederscoo, May & Smith, 2010; Stürmer, 2012; van der Heijden et al., 2015) (Figs 1 and 3). Of these, the most important group is the Glomeromycota, among which nearly all described species form arbuscular mycorrhizal associations. Fossil evidence indicates that mycorrhizal associations were present in the 400 million year old Rhyic Chert and implies that fungal interactions were essential for plant terrestrialization (Dotzler et al., 2006, 2009; Strullu-Derrien et al., 2014; Berbee, James & Strullu-Derrien, 2017). The genera Geosiphon and Densospora are currently key to solving the puzzle of mycorrhizal evolution. It is possible that Glomeromycota evolved from Geosiphon-like associations with cyanobacteria or ancestors of land plants. Within this line of reasoning, some authors have proposed that the enigmatic Prototaxites could have been a symbiotic Geosiphon-like organism (Retallack & Landing, 2014). However, Geosiphon is placed in a well-resolved group of mycorrhizal-forming fungi, making very likely that this association evolved secondarily (Schüssler et al., 2007). If *Densospora*, currently of uncertain phylogenetic placement, is affiliated to Glomeromycota it would represent the only member of the group known to form ectomycorrhizal associations. If, on the other hand, *Densospora* is a member of the Mucoromycota, perhaps the Endogonales, it might provide deeper insight into the evolution of mycorrhizae in the Mucoromycota and might suggest a mycorrhizal origin for the whole phylum. This possibility seems most consistent, as certain lines of evidence point to Endogonales (Mucoromycota) as the first mycorrhizal fungi (Read et al., 2000; Bidartondo et al., 2011; Field et al., 2015). The debate is still ongoing, and some studies point to an association between Glomeromycota and the first land plants (Rimington et al., 2018). Fine endophytes form a morphologically distinct type of association with plants traditionally considered as a
type of arbuscular mycorrhiza. Strikingly, molecular analyses of the fine endophyte *Glomus tenue* showed that this species is actually a member of the Mucoromycota, related to liverwort symbionts in the Endogonales (Orchard et al., 2017).

With the exception of Endogonales, ectomycorrhizal fungi seem to have originated more recently and independently in several groups (Hibbett & Matheny, 2009; Tedersoo, May & Smith, 2010; van der Heijden et al., 2015).Only a minor fraction of plants form this kind of mycorrhizal association and most are trees, meaning that ectomycorrhizae are important in forest environments. In stark contrast with the limited number of plant species with which they associate, ectomycorrhizal fungi show high diversity. This diversity is well described, as most of these fungi produce macroscopic fruiting bodies. Finally, the plant family Orchidaceae is a hyperdiverse clade that forms highly specific mycorrhizal associations with a great diversity of fungi (Sathiyanadash et al., 2012; van der Heijden et al., 2015; Pellegrino, Luca & Bellusci, 2016). Unlike Glomeromycota and the Endogonales, these fungi tend to have a relatively low dependency on their plant hosts.

The biotrophic nature of Glomeromycota greatly impedes genomic studies. Until recently there was only one species sequenced in this group: *Rhizophagus irregularis* (syn. *Glomus intraradices*). Its genome is fairly large (153 Mbp), encoding around 28300 genes. Unlike parasitic biotrophs, *R. irregularis* has not lost most metabolic pathways, although the genome is reduced in carbohydrate-degrading enzymes and toxin-biosynthesis pathways (Tisserant et al., 2012, 2013; Kuo et al., 2014). The genome includes expansions in regulatory proteins and a high proportion of transposable elements (Lanfranco & Young, 2012; Tisserant et al., 2012, 2013). It is important to note that *R. irregularis* has an extremely broad host range and is one of the very few members of the Glomeromycota that can be grown in culture. Recent genomic studies of additional species in this group (*Rhizophagus clarus*, *Rhizophagus cerebriforme*, *Diversispora epigaea*) shows that these traits are widespread (Chen et al., 2018; Sun et al., 2018; Morin et al., 2019). No genome of a member of the Endogonales is currently published. Several ectomycorrhizal members of the Agaricomycetes have now been sequenced (Kohler et al., 2015). Comparative genomics has shown that these fungi tend to be similar in gene content and structure to related organisms, although they contain a reduced carbohydrate-metabolism gene pool and highly variable and lineage-specific ‘symbiosis-toolkit’ genes (Martin et al., 2008; Martin & Nehls, 2009; Kuo et al., 2014; Kohler et al., 2015).

Endophytic fungi are ubiquitous components of natural environments, affecting virtually all plant species (Faeth & Fagan, 2002; Rodriguez et al., 2009; Sun & Guo, 2012; Hardoin et al., 2015; Wani et al., 2015). These interactions are highly specific, and many fungal species can colonize the same plant. Fungal endophytes are very common in non-lichenic Pezizomycotina, but can be found in most fungal lineages. Endophytes in the order Hypocreales deserve special note. This group includes many important plant pathogens, invertebrate parasites and mycoparasites, and are common producers of toxins, alkaloids and other secondary metabolites. The endophytic lifestyle in genera such as *Claviceps* probably evolved from insect-pathogenic ancestors (Spatafora et al., 2007) (Fig. 4). Studies of this group influenced early classifications of endophytic lifestyles, dividing them into clavicipitaceae and non-clavicipitaceae (Rodriguez et al., 2009; Porras-Alfaro & Bayman, 2011; Hardoin et al., 2015). Many endophytes occupy other ecological niches, acting as parasites, saprotrophs or epiphytes (Rodriguez et al., 2009; Rai & Agarkar, 2014; Hardoin et al., 2015) (Fig. 4). Epiphytic communities include fungi and bacteria living on the surface of leaves and other parts of plants (Hardoin et al., 2015; Vacher et al., 2016; Datlof et al., 2017). These communities are radically different from the endophytic communities separated from them by mere millimeters of plant tissue, although some species might be found in both environments (Santamaria & Bayman, 2005; Porras-Alfaro & Bayman, 2011). Comparative genomic studies of these ecotypes are difficult to perform, as it is virtually impossible to prove that a particular fungus is not an undescribed endophyte or epiphyte in the wild.

Several early-diverging lineages within Dikarya have members that are root endophytes (Figs 1 and 3): Entorrhizomyctera, Archaeorhizomyctera (Taphrinomycotina), some Pezizomyctera (Pezizomycotina) and probably Neol ectomyctera (Taphrinomycotina). This implies that roots rapidly became an important niche for fungi, and most clades independently became endophytes by the time plants occupied land (Fig. 4). Alternatively, the common ancestor of all Dikarya might have been an endophyte of land-plant ancestors. Most endophytic communities are very similar to those found growing inside lichens (U’Ren et al., 2010). In a broader evolutionary perspective, this observation suggests another possible route by which plant-associated fungi evolved before vascular plants existed. These fungi could have inhabited lichens, which were then a more significant component of the community, from which they moved to newly evolving vascular plants. Endophytic and epiphytic communities are poorly explored sources of fungal biodiversity, but there is evidence of a latitudinal gradient of diversity in these communities, reaching maximum diversity in tropical areas (Arnold & Lutzoni, 2007; Aime & Brearley, 2012). The use of molecular techniques has led to the discovery of several new fungal lineages in recent years: Xylonomycetes (Gazis et al., 2012), Phaeomoniellales (Chen et al., 2015), Archaeorhizomyctera (Rosling et al., 2011) and Talbotiomycetales (Vánky, Bauer & Begerow, 2007; Riess et al., 2015). Thus, it is highly likely that a great diversity still remains to be discovered among plant-associated fungi.

(3) Plant parasitism

Plant parasitism is extremely common among fungi, appearing in different forms in most fungal lineages (Figs 1 and 3). Broadly, two main types of plant pathogens exist:...
necrotrophic and biotrophic. Necrotrophic plant pathogens penetrate the plant tissue, producing necrosis and feeding on the dead tissue. Biotrophic pathogens display specialized mechanisms to avoid plant defences and gather resources from the tissue without killing it. In some cases fungi utilize both strategies at different stages of the life cycle, termed hemibiotrophy. The division between a symbiont, a mutualistic endophyte, and a parasite is quite blurred, and there is growing evidence that even archetypal pathogens might also exist in non-infectious relationships with plants (van Kan, Shaw & Grant-Downton, 2014; Lofgren et al., 2018). While generalizations are inaccurate given the vast diversity of both fungal pathogens and their relationships with their hosts, this broad division allows us to draw some conclusions regarding their evolutionary trends.

Necrotrophic plant pathogens must colonize the tissue faster than the plant can defend it. Such fungi express a wide array of virulence factors such as effector proteins, carbohydrate-hydrolysing enzymes, proteases, and toxins that help them invade (Mengiste, 2012; Zhao et al., 2013; Wang et al., 2014a). Fungi also need to access a sufficient supply of bioelements (nitrogen, phosphorus, iron and other trace elements) that would otherwise limit their growth. Effector proteins, which are secreted fungal proteins that interfere with plant regulatory mechanisms, promote relocation of host resources and inhibition of host defences. As fungal effectors must interact with host regulatory proteins to exert a function, there is generally strong co-evolution (i.e. an arms race) between these factors that may promote host specialization. Conversely, a higher range of effectors might make the fungus successful in a wider range of potential hosts. Other secreted proteins such as hydrolysing enzymes, in combination with a plethora of transporters and siderophores allow the fungus to derive nutrients from the host (Dodds, 2010; Amselem et al., 2011; Marcet-Houben et al., 2012; O’Connell et al., 2012; Wang et al., 2014a; Sillo et al., 2015). Many necrotrophs exist in the environment as saprotrophs, becoming infectious occasionally and particularly when the plant is under stress. The presence of different lifestyles in the same species imply specific challenges regarding gene content and regulation. Such factors are likely to result in an increased genome size, which in turn requires a higher nutritional intake to meet DNA biosynthesis and the production of dispersion structures. Thus, as a general rule, host-restricted necrotrophic plant pathogens tend to have smaller genomes and fewer protein-coding genes than broad-spectrum pathogens (Marcet-Houben et al., 2012; O’Connell et al., 2012; Jilca et al., 2016; Schuelke et al., 2017).

The above examples are for necrotrophic plant pathogens in the Pezizomycotina, which are highly diverse and well studied. Very few necrotrophic members of the Basidiomycota have been sequenced to date, and most plant-pathogen lineages in Basidiomycota are biotrophic (Puccinomycotina, Ustilaginomycotina). Nectrophors are common in Agaricomycotina, but many are associated with woody plants and tend to be difficult to culture under laboratory conditions. In addition, Basidiomycota are usually heterokaryotic, adding complexity to genomic studies. *Rhiocactonia solani* is an important necrotroph that has been extensively studied (Wibberg et al., 2013; Zheng et al., 2013; Hane et al., 2014). Genome studies are also available for *Moniliophthora* spp., which have marked transcriptional differences between the biotrophic and necrotrophic growth forms (Mondego et al., 2008; Rincones et al., 2008; Meinhardt et al., 2014). These cases suggest that many mechanisms will have emerged independently in Ascomycota and Basidiomycota. Pathogenic wood-decaying fungi in the Agaricomycetes evolved primarily as lignin degraders but occasionally developed the ability to infect healthy trees (Olson et al., 2012; Sigoillot et al., 2012; Ohm et al., 2014; Riley et al., 2014) (Fig. 4). This category includes the genus *Armillaria*, which is perhaps the most morphologically complex fungus yet known. *Armillaria* is able to form root-like multicellular structures (rhizomorphs) that allow the fungus to disperse asexually and relocate nutrients over vast networks. The ability to produce rhizomorphs corresponds with genomic expansion and re-utilization of fruiting body networks. The ability to produce rhizomorphs corresponds with genomic expansion and re-utilization of fruiting body and mycelial regulatory networks (Sipos et al., 2017; Sipos, Anderson & Nagy, 2018).

The situation is considerably different for biotrophic plant pathogens. Biotrophs rarely need to spread quickly, relaxing the trade-off of genetic toolkit versus genome size. Compared with necrotrophs they show a higher dependency on the host and a reduced armoury of hydrolytic enzymes and other aggressive mechanisms (Zhao et al., 2013; Okmen & Doehlemann, 2014; Qhanya et al., 2015), meaning that biotrophs tend to conform with the usual evolutionary trend of parasitic genome reduction. Indeed, these pathogens tend to have reduced gene numbers and have lost many metabolic pathways, particularly those involved in biosynthesis of secondary metabolites or of compounds that can be obtained from the host (Kämper et al., 2006; Wicker et al., 2013; Jones et al., 2014; Toome et al., 2014; Perlin et al., 2015). Despite this, inflated genomes are known in some of these lineages, often mediated by the accumulation of repetitive elements rather than increases in gene content (Raffaele & Kamoun, 2012; Dong, Raffaele & Kamoun, 2015). For example, 90% of the 125 Mbp genome of *Erysiphe necator* is composed of transposable elements (Jones et al., 2014; Wang et al., 2015a). It is important to note that not all biotrophic parasites are exclusively dependent on the host. As an illustration, consider the smut fungus *Ustilago*. This fungus can be found in soil as a free-living yeast, and can be cultivated easily, although it requires the plant host to complete its life cycle. Curiously, *Ustilago* and related genera show unusually high genome compaction, preserving most of their primary metabolic pathways intact (Kämper et al., 2006; Wollenberg & Schirawski, 2014), and suggesting that the saprotrophic stage might impose genome size restrictions. Finally, it is important to note that expanded genomes and difficulties regarding *in vitro* culture make genomic studies harder for biotrophic fungi, despite their obvious economic interest.
Host specificity can also be driven by pathogenesis islands containing genes for the synthesis of specialized toxins and other effectors. These islands tend to concentrate in certain chromosomal regions or even in specific small chromosomes, and tend to evolve at a rapid rate, generating what has been termed the ‘two-speed evolution model’ (Dong, Raffaele & Kamoun, 2013). Genes within these regions can be transferred easily, and in some cases the whole region is mobile and can jump between related species or strains (Akagi et al., 2009; Coleman et al., 2009; Mehrabi et al., 2011; Van Der Does & Rep, 2012; Vlaardingerbroek et al., 2016; Mehrabi, Mirzadi Gohari & Kema, 2017). Exchange of pathogenic effectors provides an effective mechanism for host switching and, at least between closely related strains, might be mediated by sexual or parasexual mating. The existence of these regions, which tend to have a specific composition and highly repetitive content, imposes a heavy challenge to genome studies. On top of being frequently misassembled, these regions are full of rapidly evolving, taxonomically restricted, and horizontally transferable genes. Since these situations require particular approaches to be detected and subsequently studied, it is likely that many important pathogenic factors have been missed – hidden as assembly artefacts, mispredicted genes or uncharacterized proteins. Finally, hybridization is another important source of genomic instability and has been associated with the diversification of some plant pathogens (Park & Wellings, 2012; Stuknenbrock et al., 2012; Depoetter et al., 2016; Stukenbrock, 2016). In both cases, the evolutionary consequences are significant, allowing rapid adaptation to novel environments and hosts.

(4) Wood rot fungi

Terrestrial ecosystems are dependent on carbon fixation by land plants. Cellulose and similar polysaccharides are the main carbon-containing components of plant tissues. These carbon compounds can be degraded by many different groups of organisms, including many fungal lineages. However, an important fraction of plant carbon is accumulated in the form of highly complex aromatic heteropolymers collectively termed lignin (Thevenot, Dignac & Rumpel, 2010). Lignin is particularly abundant in woody plants, which represent a significant proportion of plant biomass in most terrestrial ecosystems. This family of compounds is highly stable, largely insoluble and mechanically strong (Martinez et al., 2005). Due to these qualities lignin derivatives can accumulate in soils and form an important fraction of soil organic matter (Thevenot, Dignac & Rumpel, 2010).

The ability enzymatically to degrade lignin compounds has evolved only once in the biosphere, within the class Agaricomycetes (Dashtban et al., 2010; Lundell, Måkelä & Hildén, 2010; Floudas et al., 2012; Sigoillot et al., 2012) (Fig. 4). Fungi that manifest this ability are known as white rot fungi, due to their ability to remove the dark lignin from wood materials. Wood-decaying fungi without this capability are termed brown rot fungi. It is important to note that this distinction is only approximate, as fungi with partial lignin degradation capabilities are known (Gilbertson, 1980; Seifert, 1983; Nilsson et al., 1989; Worral, Anagnost & Zabel, 1997; Riley et al., 2014; Nelsen et al., 2015; Krah et al., 2018). There is also a clear tendency towards specialization in both groups, with brown rot fungi usually generalists or gymnosperm specialists and white rot fungi usually angiosperm specialists (Krah et al., 2018). The acquisition of this ability is related to a huge expansion of secreted laccases and heme-peroxidases, that produce highly oxidative species to attack the chemical structure of lignins (Martinez et al., 2005; Lundell, Måkelä & Hildén, 2010; Floudas et al., 2012; Guerriero et al., 2015; Treseder & Lennon, 2015). It has been proposed that the ability to degrade lignin evolved in response to the accumulation of lignomaterials during the Carboniferous, and that the novel ability to exploit this carbon sink greatly affected global carbon cycles and propelled the diversification of the Agaricomycetes (Floudas et al., 2012). This idea of a sudden acquisition of this ability by fungi has found detractors that consider that lignin itself could not have evolved instantaneously in land plants (Nelsen et al., 2015).

VII. MORE THAN THE SUM OF THEIR PARTS: LICHENIZED FUNGI

Symbiosis is the mutually beneficial association between two or more organisms. This concept was first proposed by Anton de Bary in the second half of the 19th century (Oulhen, Schulz & Carrier, 2016) after studying microscopic preparations of lichens. Lichens are macroscopic formations formed by a tissue of fungal origin, the mycobiont, that encapsulates a phototrophic cyanobacteria or chlorophyte, the photobiont. They can be found in all terrestrial biomes, and are particularly abundant and diverse in environments hostile to other photosynthetic lifeforms, such as high-elevation mountains, tundra and deserts. The mycobiont is highly resistant to irradiation and desiccation, requires no substrate and is able to obtain carbon, and sometimes nitrogen, from the photobiont; for which it provides a protective environment. Around 6–8% of the land surface of the Earth is covered by lichens, which play important global biogeochemical roles (Gadd, 2006, 2010; Asplund & Wardle, 2017). Lichens are largely restricted to Pezizomycotina (Fig. 3), of which nearly half (around 20,000 species) have adopted this lifestyle (Sipman & Aptroot, 2001). Lichens have representatives in six classes of Pezizomycotina, of which the Lecanoromycetes and the Arthoniomycetes are the two most species-rich lichen-forming clades (Grube & Wedin, 2016). Reported cases of lichens in several groups of Basidiomycota were traditionally regarded as anecdotal. However, taxonomic re-evaluation of the basidiolichen Dyctionema glabratum revealed a minimum of 126 previously unrecognized species (Lücking et al., 2014), and thus basidiolichen diversity is probably hugely underestimated. Lichens contain a high diversity of other microbes in association, including other fungi. It has been proposed that
an endolichenic lifestyle might represent an intermediate step between saprotrophy and endophytism (Arnold et al., 2009) (Fig. 4). Some of these associated microbes are parasites, including other lichen species that colonize the thallus and slowly replace it (Lawrey & Diederich, 2009). Endolichenic fungi might have phenotypic effects on the overall thallus. This is certainly the case for the lecanoromycete Bryoria sp. (Spribille et al., 2016), and drastic changes in lichen taxonomy may be likely.

The lichen fossil record is very ancient, dating at least to the Devonian (Karatýgin, Snigirevskaya & Vikulin, 2009; Honegger, Edwards & Axe, 2013), although a lichenic nature has been proposed for some Ediacaran fossils and lichen-like forms might have been among the first terrestrial fungi (Retallack, 2012). Winfeniatia reticulata is a fossil from the Early Devonian that has been interpreted as a zygomycetous lichen (Karatýgin, Snigirevskaya & Vikulin, 2009; Krings, Taylor & Dotzler, 2013). If correct, this would imply that lichenization pre-dates the divergence of Dikarya, or at least appeared independently in other lineages. The main modern lichen-forming lineages diversified at least as early as the Carboniferous (Prieto et al., 2013a, 2013b). It is unclear how many times the lichen lifestyle has appeared in the Ascomycota. Some early studies proposed a single event, followed by multiple independent transitions to a saprotrophic habit (Lutzoni, Pagel & Reeb, 2001). Multiple origins is the currently favoured view, although there is no consensus on the number of transitions (Gargas et al., 1995; Liu, Hall & Taylor, 2004; Grube & Wedin, 2016).

Supporting this, some species can be found as both lichens and free-living saprotrophs (Wedin, Döring & Gildenstam, 2004), implying that a transition between lifestyles is possible. Lichen mycobionts are prime candidates for receiving foreign genes, given their tight association with their photobionts and with other microbes, and there is evidence that several classes of secondary metabolites unique to lichens have been horizontally transferred from bacteria (Schmitt & Lumbsch, 2004), implying that a transition between lifestyles is possible. Lichen mycobionts are prime candidates for receiving foreign genes, given their tight association with their photobionts and with other microbes, and there is evidence that several classes of secondary metabolites unique to lichens have been horizontally transferred from bacteria (Schmitt & Lumbsch, 2004). Lichens can also donate genes to their photobionts, as has been inferred for several genes in the Trebouxiophyceae (Beck et al., 2015).

Several peculiarities have meant that lichen mycobionts lag behind other fungi in terms of genome studies. Lichens are composite organisms, requiring either independent culture of the mycobiont or the use of metagenomic-like approaches (Meiser et al., 2017). Independent culture limits studies on the symbiosis itself and carries an array of challenges in terms of sustaining the mycobiont under laboratory conditions. Metagenomic approaches are far more complex, both experimentally and computationally, and can lead to fragmented assemblies and contamination problems. Genomic sequencing and comparative analyses in the euromycete Endocarpon pusillum revealed several traits putatively related to symbiosis (Wang et al., 2014). Its genome has only a small secretome and a reduced number of sugar transporters, but has undergone expansions in gene families encoding nitrogen and magnesium transporters, cell-signalling pathways and proteins involved in protection against desiccation. Enhancing nitrogen transport seems to be important in lichenization, at least in fungi whose photobiont partner is not capable of nitrogen fixation, and both gene duplication and HGT seem to play a role in such gene expansions (McDonald et al., 2013; Wang et al., 2014b). Genomes of several lichen-forming fungi are now available with varying degrees of completeness and quality, although no comparative studies have been published yet (Grube & Wedin, 2016).

Black fungi, also known as black yeasts or black meristematic fungi, comprise an assemblage of lineages within the Pezizomycotina, mostly in the orders Capnodiales, Pleosporales, Myriangiales and Dothideales within the Dothideomycetes (Ruibal et al., 2009) and in the orders Chaetothyriales and Verrucariales in the Eurotiomycetes (Teixeira et al., 2017) (Fig. 3). These fungi are characterized by extreme melanization and adaptation to growth under oligotrophic and highly stressful conditions. In all cases they are characterized by the accumulation of melanins, from which derives the name black fungi. These fungi can live in a wide range of temperatures and can proliferate under near-total desiccation, including in some cases in concentrations of inorganic salts close to saturation (Gostiničar et al., 2012; Sellmann et al., 2015; Moreno, Vicente & de Hoog, 2018). They are also highly tolerant to ionizing radiation, extreme pH, mechanical force, heavy metals and other toxic compounds. They have very low metabolic requirements and slow growth, but they are often able to exploit extremely resilient nutrient sources (Sellmann et al., 2015; Moreno, Vicente & de Hoog, 2018). They tend to associate with biofilm-forming bacteria to form extremely resistant microbial communities (Mori et al., 2014; Kirchhoff et al., 2017; Zapantčík et al., 2018). Their morphology is quite variable, and many species are dimorphic. Spherical shapes minimize the surface/volume ratio and thus are favoured in many harsh environments (Sterflinger & Krumbein, 1995; Gorbushina, Kotlova & Sherstneva, 2008). Due to their tolerance they can be found in virtually any environment although in non-extreme conditions, where other faster-growing microbes can proliferate, they are relegated to low abundance. Many of these fungi seem to inhabit small pores in inert materials, including anthropogenic environments such as ceramics, glass, steel or concrete. Due to their exceptional resistance, black fungi have been proposed to be prime candidates for colonizing other planets (Onofri et al., 2007; Scalzi et al., 2012; Sellmann et al., 2015). Some species can infect exposed surfaces on animals, causing dermatological and opportunistic infections in vertebrates, including humans (e.g. athlete’s foot, tinea nigra) (Revankar & Sutton, 2010; Chowdhary, Perfect & de Hoog, 2014; Seyedmousavi et al., 2014), and in invertebrates (Vakili, 1993; Van Dover et al., 2007; Vicente et al., 2012). Black fungi are also common components of epiphytic
communities, although they are very rarely able to infect the plant (Datlof et al., 2017; Teixeira et al., 2017). Finally, in recent years a wide diversity of Chaetothyriales and Capnodiales associated with ant nests has been described (Voglmaier et al., 2011).

The main unifying characteristic of black fungi is the accumulation of melamins, a generic term used to describe a diverse set of natural pigments. Melamins act as powerful protectors against oxidative damage, ionizing radiation and other damaging chemical and physical conditions. Black fungi bind melamins to their bio-molecules, particularly their cell walls, in ways that are not fully understood. Apart from melamins, these fungi tend to accumulate soluble compounds that provide protection, such as mycosporines, trehalose, polyalcohols, betaine, proline and diverse carotenoid pigments (Gorbushina, Kolova & Sherstneva, 2008; Moreno, Vicente & de Hoog, 2018). Some of these fungi can grow using unorthodox organic compounds as carbon sources, such as toluene or plastic materials (Revankar & Sutton, 2010). Some observations even suggest that some of these fungi could use sources of ionizing radiation to obtain chemical energy and even perhaps fix atmospheric carbon (Dadachova et al., 2007; Gostinčar et al., 2012). Light-sensing proton pumps have been described for some species (Waschuk et al., 2005; Garcia-Martinez et al., 2015) that have been proposed to be functionally similar to prokaryotic bacteriorhodopsins. While fungi lack a Calvin cycle, carbon fixation could be performed by at least undescribed metabolic pathways. Alternative carbon-fixation pathways exist in prokaryotes, some of which might have arisen independently or have been acquired by HGT in fungi. For example, a hypothetical pathway able to use photo-chemical energy to reduce CO₂ to other single-carbon compounds could be derived easily from methylotrophic pathways, which are known in some fungi. Even if the efficiency of such pathways is very low, it would provide an important advantage in oligotrophic environments (Gostinčar et al., 2012).

Unfortunately, research on black fungi is hampered by their slow growth, resistance to genetic manipulation and perhaps by a focus on human-pathogenic species. Their extremely resistant cells make DNA extraction very difficult, even from axenic samples (Marzban, Tesei & Sterflinger, 2013). Despite this, dozens of genomes from black fungi are now available. Their genome size is very similar in size, content and composition to the other black fungi considered. These results imply that either these diverse environments impose similar ecological challenges for black fungi (for instance, low water activity or high irradiation), that their adaptations are useful in a wide range of conditions, or that their peculiarities might be mediated by uncharacterized adaptations are useful in a wide range of conditions, or that their peculiarities might be mediated by uncharacterized mechanisms (Sterflinger et al., 2014). However, since their polyextremophilic properties emerge due to accumulation of chemical compounds and control of universal traits such as membrane fluidity, phenotypic variation should be easy without extensive genomic innovation.

Molecular-dating analyses (Gueidan et al., 2008) suggest that black fungi in the Dothideomycetes diversified during the late Devonian, while Chaetothyriales are more recent, dated to the middle Triassic. Both geological ages are characterized by widespread desertification of continental landmasses. Black fungi in both Dothideomycetes and Eurotiomycetes are phylogenetically related to lichen-forming fungi (Ruibal et al., 2009; Schoch et al., 2009; Teixeira et al., 2017) (Fig. 4). Given the extreme resistance to adverse conditions manifested by both ecotypes and the close phylogenetic affinity of black fungi in both Dothideomycetes and Eurotiomycetes with largely lichenized orders, it has been hypothesized that there is a functional relationship. Some black fungi are able to form microbial communities with diverse bacteria, including cyanobacteria, and some authors have proposed that these associations represent a protolichen (Gorbushina, Beck & Schulte, 2005; Gueidan et al., 2008; Ruibal et al., 2009; Gostinčar et al., 2012). In any case, many black fungi live within the thallus of lichens, where they might be relatively protected from the environment, and are exposed to the secondary metabolome of the lichen (Fig. 4). Finally, it has been proposed that an ant-association lifestyle might have played an important role in the diversification of the Chaetothyriales (Voglmaier et al., 2011; Blatrix et al., 2017; Moreno, Vicente & de Hoog, 2018), although there is little evidence for the existence of ant-specialized Chaetothyriales (Blatrix et al., 2017). Ants produce a diverse array of toxic compounds, and it has been hypothesized that the peculiar metabolic capabilities of black fungi might have evolved in association with ant nests (Moreno, Vicente & de Hoog, 2018).
IX. THE YEAST LIFESTYLE

The term ‘yeast’ is used to describe any fungus that reproduces asexually by budding or fission, producing single-cell stages, and has sexual structures not enclosed in a fruiting body (Kurtzman & Sugiyama, 2015). This general definition is often widened to include dimorphic lineages that produce mycelial growth in their sexual stages and is even occasionally used to embrace biotrophic pathogens and black yeasts. The traditional model yeasts Saccharomyces (Saccharomycotina) and Schizosaccharomyces (Taphrinomycotina) do in fact share several ecophysiological and even genomic characteristics with several of these lineages that deserve discussion. We propose herein that the ‘yeast lifestyle’ is a label that can be applied to the lifestyle of a unicellular or dimorphic fungi with a main unicellular stage in the environment and a highly limited extracellular metabolism. Yeast secondary metabolism is usually very reduced too, with only one secondary metabolic activity environments and tend to have rapid metabolism and growth. They have a reduced and compact genome, commonly including streamlined regulatory networks and with a reduced intron and intergenic content. Transition to a yeast lifestyle is often accompanied by convergent changes in regulatory networks (Nagy et al., 2014). These characteristics mean that yeast forgo the typical advantages that fungi have evolved: their ability to secrete hydrolytic enzymes, use of mycelial growth to break into a substrate, and use of complex secondary metabolites to control their surroundings. Without these traits, most yeasts inhabit environments where competition is based on the ability to exploit easily available nutrient sources rapidly, a niche typically occupied by prokaryotes. It is important to note that, as for other ecotypes we review herein, the yeast lifestyle implies a spectrum of phenotypic traits, rather than a categorical classification. Yeast-like forms can be found in Ascomycota within the Saccharomycotina, the Taphrinomycotina, and in Basidiomycota within the Pucciniomycotina and the Ustilaginomycotina (Fig. 3).

Additionally, yeast-like growth has been described at least for Schizosaccharomyces (Benny, Humber & Voigt, 2014), a poorly known fungus identified as a commensal in soil (Treseder & Lennon, 2015; Yurkov, 2018), on plant surfaces (Boynton & Greig, 2014), in the gut of insects (Blackwell, 2017), on vertebrate skin (Underhill & Iliev, 2014; Limon, Skalski & Underhill, 2017), and in marine and frozen environments (Bass & Iliev, 2014; Amaretti et al., 2014; Richards et al., 2015; Martorell et al., 2017; Rämä et al., 2017). Many have been isolated from industrial fermentations, including contaminants of food products and alcoholic fermentations (Hittinger, Steele & Ryder, 2018), sorbitol (Louis et al., 2012) and pure hydrocarbons (Buddie et al., 2011). Schizosaccharomyces is the best-studied lineage of yeasts within the Taphrinomycotina. The genus contains four species, although their genetic divergence implies the necessity for taxonomic revision (Naumov, Kondratieva & Naumova, 2015; Jeffares, 2018). Schizosaccharomyces is commonly isolated from fruit juices and other high-sugar substrates (Jeffares, 2018). At least two species of the genus, S. pombe and S. japonicus, are known to be able to switch to a limited filamentous growth form under certain conditions (Dodson et al., 2019).
Saitoella is another yeast genus within this subphylum that was isolated from soil in the Himalayas and from insect galleries in leaves (Goto et al., 1987; Kurtzman & Robnett, 2012). Environmental studies show that the genus Taphrina, typically a plant biotrophic pathogen, is also a member of antarctic soil communities (Coleine et al., 2018). Saitoella is phylogenetically related to the biotrophic plant pathogens Protonomes and Taphrina (Sugiyama, Hosaka & Suh, 2006; Kurtzman & Sugiyama, 2015), and the three genera share a low intron content, compact genome and similar gene numbers with Saccharomyces. However, some of these traits are widespread within the Taphrinomycotina, independent of their lifestyle. The recent adscription of the subphylum due to their convoluted phylogeny, the low number of described species, and the disparity in their lifestyles, makes it impossible to propose any feasible evolutionary hypothesis regarding the ecological transitions in this group.

Basidiomycetous yeasts can be found within the Pucciniomycotina and the Ustilaginomycotina. Pucciniomycotina forms the most diverse of these yeast lineages, with the yeast lifestyle evolving independently in at least four lineages (Microbotryomycetes, Spiculogloeomycolycetes, Agaricomycetes and Cystobasidimycolycetes) (Aime, Toome & McLaughlin, 2014; Wang et al., 2015b; Oberwinkler, 2017). Many of these lineages include dimorphic fungi that can be cultured as unicellular fungi, a trait that appears additionally in the Mixiomycetes and the Cryptomycolycetes, considered as yeasts by some authors. Many yeasts in the Pucciniomycotina accumulate carotenoid pigments, thus earning the common name ‘red yeasts’. Several others also accumulate lipids or possess metabolic capabilities that are not common within Saccharomyces (Frengova & Beshkova, 2009; Ageitos et al., 2011; Kot et al., 2018). These traits have raised considerable interest for their possible industrial applications. Red yeasts are cosmopolitan, with many strains isolated from cold or marine environments. These groups include endophytic strains (Firrincieli et al., 2015), and some isolates show well-developed cellularly capabilites. These fungi invariably possess small compacted genomes compared with plant-pathogenic members of the Pucciniomycotina. Red yeasts are in need of taxonomic revision, with some important genera (e.g. Rhodotorula) being clearly paraplyetic (Aime, Toome & McLaughlin, 2014; Oberwinkler, 2017). The genomes of several red yeasts are available. The typical genome size is around 20 Mbp, with 5500–7000 protein-coding genes and typically a very high GC content. Their coding density and genome size are similar to early-branching Saccharomyces, such as Varravia, although comparative genomic studies in this group are scarce. Yeast-like forms are common in asexual stages of Ustilaginomycotina. Most well-studied members of this group are plant and animal pathogens that require infection to complete their life cycle. Environmental studies suggest that yeast-like forms in the Ustilaginomycotina are common in several environments, particularly in the ocean where possible hosts are limited. This suggests that either these organisms are completely asexual, that they infect yet unknown hosts, or that they do not require a host for sexual reproduction. The phylogenetic distribution of the different lifestyles suggests that a yeast lifestyle has evolved in both Pucciniomyctina (Wang et al., 2015b; Oberwinkler, 2017) and Ustilaginomycotina (Wang et al., 2015a; Kijppornyongpan et al., 2018) several times independently from plant-pathogenic ancestors, and it is quite likely that parasitic genome reduction played a role in the first stages of yeast genome compaction. Under this hypothesis, most basidiomycetous yeasts evolved from parasitic fungi with environmentally active asexual stages that became independent from their traditional hosts (Fig. 4).

Yeasts are saprotrophic microorganisms that are unable to control a ‘territory’, rather like the majority of prokaryotes. Ecological competition with prokaryotes is unfavourable for yeasts, as their rivals tend to grow at a faster rate and have higher metabolic diversity. Low water activity has an important role in prokaryotic life. Osmotic balance requires energetic expenditure, in inverse proportion to the surface/volume ratio, which places yeast at an advantage compared to prokaryotes. Yeasts are among the main microbial components of high-osmotic stress environments containing concentrated carbon sources such as sugar (e.g. plant-derived liquids such as fruit juices, honeydew, nectar) (Pozo, Herrera & Bazaga, 2011; Lieveens et al., 2015). Some yeasts can proliferate under high concentration of inorganic salts, although their upper tolerance is comfortably surpassed by some bacteria and archaea (Gunde-Cimerman, Ramos & Piemenitaš, 2009). Yeasts, particularly from the Basidiomycota, are also common in frozen environments (Arendrup, 2013; Sellmann et al., 2014; Boetius et al., 2015; Coleine et al., 2018), in which water availability can also be limited. In addition to their role in fragile polar and mountain environments, the study of yeasts brings the potential for an industrially attractive low-temperature enzyme repertoire (Buzzini et al., 2012; Amaretti et al., 2014; Morita et al., 2014; Taskin et al., 2016; Martorell et al., 2017). Outside water-limited environments, yeasts from the Ustilaginomycotina, Saccharomycotina and Pucciniomycotina dominate marine fungal communities (Bass et al., 2007; Richards et al., 2012, 2015; Manohar et al., 2013). It has been hypothesized that these yeast communities are associated with marine ‘snow’ and other forms of highly degraded organic matter, which would imply an unexplored role in oceanic carbon cycling (Bass et al., 2007; Richards et al., 2012, 2015; Manohar et al., 2013). Many environmental yeasts appear to be lipophilic, with metabolic capabilities similar to those found in the genus Malassezia (Xu et al., 2007), which is very common in the environment (Manohar et al., 2013; Richards et al., 2015). Yeasts can also be found in association with surfaces of both vertebrates and invertebrates (see Section V). Fungi with a yeast lifestyle can be found in virtually any soil type, and even though their abundance tends to be relatively low, their diversity is considerable (Treseder & Lennon, 2015; Tedersoo et al., 2017; Yurkov, 2018).
X. CONCLUDING REMARKS

Despite their important roles in shaping ecosystems, much still remains to be understood regarding fungi. Traditional methodologies used to investigate the roles of these microorganisms in nature, such as culture-based methods or morphological characterization, are very limited. Standard isolation protocols can only obtain a fraction of natural diversity, whether because nutritional requirements are not met, inter-species relationships are broken or simply because faster growing microbes out-compete slower ones in culture environments. Morphology often reflects only poorly the genetic diversity, and requires a trained eye, which is a concern due to the worrying global trend of lack of interest in taxonomic research. Culture-independent approaches are promising, but are not without limitations. Sequence-based approaches, for example, are prone to biases and artefacts, both experimental and computational. In addition, they require considerable expenditure, infrastructure and expertise, and face strong reproducibility limitations. As a consequence, for many microbial clades, we know little more than the fact they exist, even though some are very abundant in nature.

Research on fungal evolution and ecology traditionally has been very aseptic, often merely limited to the description of numeric correlations. Microbiologists have a tendency to view their subject from a purely biochemical point of view, as abstract entities that perform metabolic transformations in nature that can be randomly sampled by sequencing technologies. But microbes, and fungi in particular, are living entities that occupy a physical space, interact with other organisms (both macro and micro), and compete over resources. Thus, they can and should be studied under the principles of traditional ecology, including niche theory and population dynamics. Fungi live and thrive within environments that are extremely different from those familiar to ecologists. We can easily imagine what life in a savannah looks like, and how a river, a mountain or a fire would affect such a setting. To understand fungi, we should do the same for the environments they inhabit, but this is no easy task. What is life like inside the gut of a beetle, in the liquid layers below a glacier, or inside the meristem of a potted plant? Furthermore, when discussing evolutionary scenarios, particularly ancient ones such as fungal terrestrialization or the origin of mycorrhizae, the available data are even more scarce. We need to be able to provide biological paradigms to interpret genomic information and anchor it to the real world.

It is necessary to gather all the information we have and use our imagination to elaborate plausible hypothetical scenarios to describe how fungi have adapted to their current niches. This fundamentally is not different from the work of 19th century naturalists. However, unlike those pioneers, who explored new lands and collected new samples, we have indirect observations, quantitative data, and imperfect experimental models. The ability to use intuition to generate a plausible description for microbial ecosystems is currently the biggest challenge in this field. This approach is similar to challenges in palaeontology, where reconstruction and extrapolation is the only way to structure a fragmented fossil record, and it is key to contextualize the biology of the organism within its setting. Stories need their characters, too, and adding ‘personality’ has always been a difficult task for microbiologists due to the limited number of phenotypic characteristics. Here, genome sequencing will represent an important tool to define the ‘identity’ of different clades. Just as a family of beetles might be defined by the morphology of their antennae or the innervation of their wings, a clade of fungi could be defined by expansions in certain protein families, peculiarities in their sequence composition, horizontal gene-transfer events and many other genomic characteristics. This approach is currently hampered by limitations in the available genomic data. However, genome description is improving, at least for some clades, such as Neocallimastigomycota or Saccharomycetales. Perhaps even more importantly, comparative genomic studies will allow us to date the acquisition of characters, enabling us to convert these genomic phenotypes into a true background that, like a character in a novel, defines how they have become who they are. This narrative approach has provided models that represent a fertile field for testing new hypotheses. And last, but not least, we need these narratives to excite and inspire future generations of mycologists.

XI. CONCLUSIONS

(1) The first fungi were zoosporic parasitoids of other unicellular eukaryotes. Nowadays, this lifestyle can be found in the Opisthosporida, Chytridiomycota and Blastocladiomycota.

(2) There are two main hypotheses to explain the process of terrestrialization in fungi. ‘Brown’ scenarios assume that fungi developed saprotrophic habits in sediments, from which they colonized soils. ‘Green’ scenarios assume that terrestrialization of fungi was intimately linked to terrestrialization in green algae and Streptophyta. Here, we propose a third, ‘white’, scenario, in which fungi colonized terrestrial environments after adaptation to frozen environments.

(3) The evolutionary implications of the relationships between fungi and other microbial eukaryotes have long been overlooked. Fungi must have interacted with other fungi and protozoans during the early stages of terrestrialization. Parasitism of these organisms may have acted as a first step in the evolution of parasitism of animals.

(4) Several clades of fungi have acquired an obligatory parasitic lifestyle and show many of the typical traits that are common in parasites. Fungi are important parasites of both vertebrates and invertebrates, although the mechanisms vary greatly between the two groups. Invertebrate parasites are related to mycoparasites and amoebophagous fungi, and use their chitin-degrading abilities to attack the host. Vertebrate parasites must be able to overcome the host’s immune
responses. Pathogenesis in these lineages seems to emerge from commensalism, usually as facultative pathogens.

(5) The relationship between fungi and plants is very ancient, with fossil Glomeromycota being among the first direct evidence of terrestrial fungal life. Endophytism is a poorly explored fungal niche that holds an impressive biodiversity. Parasitism in plants falls into two main groups of strategies: biotrophy and necrotrophy. These strategies impose radically different evolutionary pressures, which is reflected in their genome characteristics. Finally, a group within Agaricomycetes deserves special mention as they developed the unique enzymatic ability to degrade lignin. This ability, whose acquisition correlates with their ability to form highly complex fruiting bodies, has granted them great evolutionary and ecological success.

(6) Compared to other fungi, lichens have been lagging behind in terms of genomic studies. The lichen lifestyle may have been key during the process of terrestrialization and is thought to be very ancient within Ascomycota, with many saprotrophic lineages being derived states. The current paradigm is shifting toward a more dynamic scenario, with the loss and acquisition of a lichenic lifestyle being much more common than previously thought.

(7) Black fungi are a highly specialized ecotype of fungi within the Dotheomyctetes and Eurotiomycetes that are able to proliferate in very hostile environments. Some of these traits are shared with lichen-forming fungi, and the two ecological types seem to be phylogenetically related.

(8) We propose a definition of the ‘yeast lifestyle’ as a prokaryote-like lifestyle in fungi. This term is not equivalent to the traditional term ‘yeast’, which should be used to describe a cellular organization. The yeast lifestyle carries several genomic traits, such as genomic compaction and secretome reduction. Yeast-like fungi have evolved independently in several lineages, and fungi with the yeast lifestyle seem to form an important fraction of microbial communities in marine, arctic and highly osmotic environments, as well as minor components on plant surfaces and in soils.

(9) While genomics has revolutionized our view of fungi, there is a growing need to merge this type of approaches with more traditional ones, such as biochemical, genetic, ecological, morphological and ontological in order to provide testable hypotheses regarding fungal biology.

XII. ACKNOWLEDGMENTS

T.G.’s group acknowledges support from the Spanish Ministry of Economy, Industry, and Competitiveness (MEIC) for the EMBL partnership, and grants ‘Centro de Excelencia Severo Ochoa’ SEV-2012-0208, and BFU2015-67107 cofunded by European Regional Development Fund (ERDF); from the CERCA Programme/Generalitat de Catalunya; from the Catalan Research Agency (AGAUR) SGR857; from the European Union’s Horizon 2020 research and innovation programme under grant agreement ERC-2016-724173; and from the Marie Sklodowska-Curie grant agreement No H2020-MSCA-ITN-2014-642095. Finally, special thanks to Alexandra Elbakyan and all her collaborators. Without their heroic labour this review would have been impossible.

Miguel A. Naranjo-Ortiz and Toni Gabaldón

XIII. REFERENCES

ACHTERMAN, R. R. & WHITE, T. C. (2013). Dermatophytes. Current Biology 23, R551–R552.

ADI, M. S. & GUPTA, V. S. (2006). Proteins in soil ecology and forest nutrient cycling. Canadian Journal of Forest Research 36, 1805–1817.

ÁGUSTINDÓN, J. M., VALLEJO, J. A., VEIGA, A., SIMÓN, P. & VILLA, T. G. (2011). Oily yeasts as oleaginous cell factories. Applied Microbiology and Biotechnology 90, 1219–1227.

AHRENDT, S. R., QUANDT, C. A., CIORANU, D., CLUM, A., SALAMON, A., ANDREPOPULOS, B., CHENG, J.-F., WOYKE, T., PELIN, A., HENRISSAT, B., REYNOLDS, N. K., BENNY, G. L., SMITH, M. E., JAMES, T. Y., GRIGOREV, I. V., et al. (2016). Leveraging single-cell genomics to expand the fungal tree of life. Nature Microbiology 3, 1417–1428.

AIMÉ, C. M. & BREARLEY, F. Q. (2012). Tropical fungal diversity: closing the gap between species estimates and species discovery. Biodiversity and Conservation 21, 2177–2180.

AMENDOLA, C., TOOME, M. & MCLAUGHLIN, D. J. (2014). 14C pneumococci. In Systematics and Evolution, pp. 271–294. Springer Berlin Heidelberg, Berlin, Heidelberg.

AKAGI, Y., AKAMATSU, H., OTANI, H. & KODAMA, M. (2009). Horizontal chromosome transfer, a mechanism for the evolution and differentiation of a plant-pathogenic fungus. Fungal Ecology 2, 1732–1739.

ALYES, D. M. C. C., TERRIBLE, L. G. & BREIT, D. (2014). The potential impact of white-nose syndrome on the conservation status of North American bats. PLoS One 9, e107395.

AMARETTI, A., SIMONE, M., QUARTERI, A., MASINO, F., RAIMONDI, S., LEONARD, A. & ROSSI, M. (2014). Isolation of carotenoid-producing yeasts from an alpine glacier. Chemical Engineering Transactions 38, 217–222.

AMSELM, J., CUOMO, C. A., VAN KAN, J. A. L., VLAUD, M., BENITO, E. P., COULON, A., COUTINHO, P. M., DE VRIES, R. P., DVER, P. S., FILLINGER, S., FOURNIER, E., GOET, L., HAHN, M., KOSHIN, L., LAPALO, N., FLUMMER, K. M., PRADI, J. M., QUEVILLON, E., SHABON, A., SIMON, P., TAN HAYE, A., TUDZYNSKI, B., TUDZYNSKI, P., WINCKER, P., ANDREWS, M., ANTOUARD, V., BRYER, R. E., REPPA, R., BENITO, I., BOUDOU, O., BRAYT, B., CHEN, Z., CHOQUEER, M., COLLEMBARE, J., COTTON, P., DANCHIN, E. G., DA SILVA, C., GAUTHIER, A., GIRAUD, C., GIRAUD, T., GONZALEZ, C., GROSSETETE, S., GUMERT, U., HEBRANT, B., HOWLETT, R. J., KODIA, C., KRETSCHMER, M., LAPPARTIENT, A., LEROCH, M., LEVIS, M., MAUL, E., NEUVILLE, C., OESER, B., PEARSON, M., POULAIN, J., POUSSEREAU, N., QUENSEVITUDE, H., RASCLE, C., SCHUMACHER, J., SEGUERES, B., SEXTON, A., SILVA, E., SIRE, C., SOARES, D. M., TALBOT, N. J., TEMPLETON, M., YANDAVA, C., YAREM, O., ZENG, Q., ROLLINS, J. A., LEBRUN, M. H. & DICKMAN, M. (2011). Genomic analysis of the necrotrophic fungal pathogen Sclerotinia sclerotiorum and Botrytis cinerea. PLoS Genetics 7, e1002230.

ANESIO, A. M., LUTZ, S., CHERIASIS, N. A. M. & BENNING, L. G. (2017). The microbiome of glaciers and ice sheets. Biofilms and Microbiofilm 3, 10.

ARAÇIO, J. P. M. & HUGHES, D. P. (2016). Diversity of entomopathogenic fungi: which groups conquered the insect body? Advances in Genetics 94, 1–39.

ARENDRUP, M. C. (2013). Candida and candidiosis. Susceptibility and epidemiology. Danish Medical Journal 60, B4698.

ARKOWITZ, R. A. & BASILIANA, M. (2011). Polarized growth in fungi: symmetry breaking and hyphal formation. Seminars in Cell and Developmental Biology 22, 806–813.

ARNOLO, A. E. & LUZTONI, F. (2007). Diversity and host range of fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88, 541–549.

ARNOLO, A. E., MAJSHEKOVSKA, J., HIGGINS, K. L., SARVATE, S. D., GUGGER, F., WAI, A., HOFSTETTER, V., KAUFF, F. & LUZTONI, F. (2009). A phylogenetic estimation of trophic transition networks of ascomycetous fungi: are lichens cradles of symbiotic fungal diversification? Systematic Biology 58, 283–297.

ARRIBARALAGA, G. & BOOTHEVOD, J. C. (2004). Role of calcium during Toxoplasma gondii invasion and egress. International Journal for Parasitology 34, 361–368.

ASPCLUD, L. & WARDLE, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. Biological Reviews 92, 1729–1739.

ASTAFEEVA, M. M. & ROZANOV, A. Y. (2012). Bacterial palaeontological study of early Precambrian weathering crusts. Earth Science Letters 1, 163–170.

ATANANOVA, I., LE CROM, S., GRUER, S., COULPIER, F., SEIDL-SEIBOTH, V., KURBICKI, C. P. & DRUZHENINA, I. S. (2013). Comparative transcriptomics reveals different strategies of Trichoderma mycoparasitism. BMC Genomics 14, 121.

BARAL, H. O., WEBER, E., MARSON, G. & QUIJADA, L. (2013). A new connection between wood saprotops and beetle endosymbiosis: the rarely reported saprobic
Evolutionary and ecological transitions in fungi

Saccharomyces is congeneric with the symbiotic yeast Symbiotaphrina (Symbiotaphrinaceae, Xylohyphales) and two assexual morphs misplaced in Hyphopogon. Mycological Progress 17, 213–254.

Barea, J. & Vivas, K. (2011). Pulmonary blastomycosis. Seminars in Respiratory and Critical Care Medicine 32, 745–753.

Barron, G. L. (1980). Fungal parasites of rotifers: a new Toxoplasmodium with underwater condensation. Canadian Journal of Botany 58, 439–442.

Bass, J. (2014). Rapid mechanisms for generating fungal diversity: whole plody shifts, aneuploidy, and loss of heterozygosity. Cold Spring Harbor Perspectives in Medicine 4, a019004.

Benn, B. G. & Garcia, C. R. S. (2011). Targeting cambium homeostasis as the therapy of Chagas’ disease and leishmaniasis – a review. Tropical Biomedicine 28, 471–481.

Bennett, R. J. (2009). A Candida-based view of fungal sex and pathogenesis. Genome Biology 10, 230.

Bennett, R. J., Forche, A. & Berman, J. (2014). Mating in yeasts: molecular mechanisms of mating and compatibility. Frontiers in Microbiology 6, 71–83.

Benny, L., Bisgrove, D., Ko, S., Do, T., Gorman, T., Hall, C., Kish, C., Kim, K., Liu, Y., Madsen, S., McNulty, M., Moon, K., Navarrete, A., Neumann, I., O’Connor, C., Pappe, C., Pinter, C., Pratap, V., Rabbiner, L., Rheinbay, E., Sambrook, J., Schmutz, J., Schwartz, M., Seidenberger, E., Stein, L., Stajich, J., Stal, A., Stewart, D., Stukenbrock, E., Tanguay, K., Torres, M., van der Vossen, E., Vlasova, A., Watanabe, T. & Yu, J. (2013). The genome of the fission yeast Clostridium botulinum. Nature 501, 179–185.

Benny, L., Bisgrove, D., Ko, S., Do, T., Gorman, T., Hall, C., Kish, C., Kim, K., Liu, Y., Madsen, S., McNulty, M., Moon, K., Navarrete, A., Neumann, I., O’Connor, C., Pappe, C., Pinter, C., Pratap, V., Rabbiner, L., Rheinbay, E., Sambrook, J., Schwartz, M., Seidenberger, E., Stein, L., Stajich, J., Stal, A., Stewart, D., Stukenbrock, E., Tanguay, K., Torres, M., van der Vossen, E., Vlasova, A., Watanabe, T. & Yu, J. (2013). The genome of the fission yeast Clostridium botulinum. Nature 501, 179–185.
Evolutionary and ecological transitions in fungi

Field, K. J., Pressel, S., Duckett, J. G., Rimington, W. R. & Bidartondo, M. I. (2015). Symbiotic options for the conquest of land. Trends in Ecology & Evolution 30, 477–486.

Firrincieli, G. & Allard, N. (2013). High-throughput differentiation of Fusarium avenaceum, an aggressive species in rice crops. Mycologia 105, 92–103.

Gadd, G. M. & Pressel, S. (2006). Evolutionary transitions from pathogenic to mutualistic relationships in the entomophthoromycotan fungi. Mycological Research 110, 409–420.

Gleason, H. A. (1998). Plant Ecological Communities. Oxford University Press, New York.

Golyshina, O. Y. & Widegren, A. (2005). Ecological and evolutionary significance of the fungal endophytic lifestyle. Microbial Ecology 50, 338–347.

Gorbaruk, M. A., Humber, R. A. & Varga, J. T. (2015). Phylogenetic insights into fungal endophytes. Frontiers in Microbiology 6, 1–12.

Gorick, D. A., Ostfeld, R. S., Varga, J. T., Ratcliffe, N. D., Novotny, M. E., Sogin, M. L. & Hoberg, E. P. (2015). Molecular and ecological differences between mycobiomes of seashore and freshwater habitats. FEMS Microbiology Ecology 100, 1–11.

Grimm, V. K., Yayanos, A. O., Colburn, A. J., Dite, A. L., Rice, C. D. & Voldner, S. (2016). Evolutionary methods of Fe nutrition in Bacteria and Eukaryotes. Microbiology 162, 1–14.

Gryganskyi, A. P., Humber, R. A., Smith, A. M., Siddiqui, F., Voigt, M. G., Varga, J. T. & Varga, J. T. (2015). The hidden world of thalloid fungi. Frontiers in Microbiology 6, 1–12.

Gundlach, M. M., Arnold, A. S., Albers, K. & Forstner, F. W. (2015). Diversity and distributions of eukaryotic microorganisms in the ocean. Frontiers in Microbiology 6, 1–12.

Hameed, M. A., Syed, Z., Iqbal, Z., Ali, M. & Dar, W. S. (2015). Taxonomic status of the orange bread mold Aspergillus fumigatus. Mycological Research 119, 1–8.

Hamamoto, Y., Kashiwagi, K., Kato, S., Kato-Paterson, S. & Satoh, C. (2015). Comparative genomics of the fungal endophytic yeast Rhodotorula glutinis isolated from different plant species. Frontiers in Microbiology 6, 1–12.

Hardie, P. R. (2013). The evolution of plant-microbe interactions in the past and future. Frontiers in Microbiology 4, 1–12.

Harkonen, P. T. & Vargas, J. T. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Harrington, B. J., Dierking, B. J., Hall, A. M., Sorensen, D. M. & Aldrich, R. W. (2016). A comparative metagenomic analysis of bacterial communities from the human oral cavity. Journal of Microbiological Methods 122, 1–12.

Haug, W., Treffinger, M., Tischer, C., Huser, T., Fröhlich, A., Oehmichen, S. & Rüdiger, E. (2015). Systematic and molecular analysis of the fungal endophytic Yeast Rhodotorula glutinis isolated from different plant species. Frontiers in Microbiology 6, 1–12.

Hay, R. J., Castañeda-Moya, S., Zsom, A. & Varga, J. T. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Hecht, K. L. & Forstner, F. W. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Helgason, B., Steens, J., Ingólfsson, B., Gislason, J., Sigurðsson, M., Sigurjónsson, Á., Helgason, T., Jónsdóttir, K. & Ólafsdóttir, A. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Hirose, M. & Takahashi, Y. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Hoefer, M., Kursa, M. B., Rokicki, S., Dabrowski, W. & Hall, M. A. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Hoffman, J. E., Newman, D. K., Kinross, R. J., Cotter, P. D., Hickey, J. F., O’Toole, G. A., Forsythe, T., Chawla, A. & O’Toole, G. A. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

HOF, M. & NAVRATIL, S. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Holmes, C. R., Smith, A. M., Siddiqui, F., Varga, J. T. & Varga, J. T. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.

Huang, Y. & Goh, J. J. (2015). The hidden world of the soil. Frontiers in Microbiology 6, 1–12.
within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiology and Molecular Biology Reviews 79, 293–320.

Hans, H., Taylor, T. N. & Remy, W. (1994). Fungi from the Lower Devonian Rhynie Chert: mycoparasitism. American Journal of Botany 81, 29–40.

Hassler, H. B. & Grube, M. A. (2018). Chytrids dominate arctic marine fungal communities. Environmental Microbiology 18, 2001–2009.

Hausser, P. M., Burdet, F. X., Cisné, O. H., Keller, L., Taffé, P., Sanglard, D. & Pagni, M. (2010). Comparative genomics suggests that the fungal pathogen pneumocystis is an obligate parasite scavenging amino acids from its host’s lungs. PLoS ONE 5, e11352.

Haves, G. E. & Novak-Frazer, L. (2016). Chronic pulmonary aspergillosis—where are we? and where are we going. Journal of Fungi 2, E18.

Heimits, J., Carter, D. A., Dyer, P. S., Soll, R. D., Kwon-chung, K. J., Fraser, J. A., Tamara, L., Römer, T., Krysan, D. J., White, T. C., Finkiel, K. & Thomas, L. (2018). Sexual reproduction of human fungal pathogens. Cold Spring Harbor Perspectives in Medicine 4, 1–20.

Henk, D. A. & Fisher, M. C. (2012). The gut fungus Basidibulosum vannamei has a large number and different copy numbers of putatively functionally redundant elongation factor genes. PLoS ONE 7, e31269.

Henk, D. A. & Vilgalys, R. (2007). Molecular phylogeny suggests a single origin of symbiosis in the Pucciniae/mycetes with support for some relationships within the genus Septobasidiomycetes. American Journal of Botany 94, 1513–1526.

Herbert, P. F., Hagen, F., Pinheiro, R. L., Muro, M. D., Meis, J. F. & Queiroz-Telles, F. (2017). Ecopeediology of Cytopsopus gutti in developing countries. Journal of Fungi 3, E2.

Hibbett, D. S. & Matheny, P. B. (2009). The relative ages of ectomycorrhizal mushrooms and their plant hosts estimated using Bayesian relaxed molecular clock analyses. BMC Evolutionary Biology 9, 117–124.

Hittinger, C. T., Rokas, A., Bai, F., Boekhout, T., Gong, P., Jeffries, T. W., Libkind, D., Kominek, J., Kurtzman, C. P. & Rosa, C. A. (2015). Genomics and the making of yeast biodiversity. Current Opinion in Genetics & Development 35, 100–109.

Hittinger, C. T., Steele, J. L. & Ryder, D. S. (2018). Diverse yeasts for diverse fermented beverages and foods. Current Opinion in Biotechnology 49, 199–206.

Hoffman, P. F., Abbott, D. S., Ankenay, Z., Bennett, D. L., Brooks, J. J., Cohen, P. A., Cox, G. M., Creveling, J., Donnadeye, Y., Erwin, D. H., Fairchild, I. J., Ferreira, L. M., Fiedler, J. C., Hall, V. G. P., Jensen, M. F., et al. (2017). Snowball Earth climate dynamics and Cryogenian geology-geobiology. Nature 550, 1–12. https://doi.org/10.1038/nature24365.

Holman, L. M., Schröder, M. S., Turner, S. a., Taff, H., Andres, D., Gröger, Z., Gäcker, A., Ames, L., Haynes, K., Higgins, D. G. & Butler, G. (2014). Comparative phenotypic analysis of the major fungal pathogen Candida parapsilosis and Candida albicans. PLoS Pathogens 10, e1004365.

Honegger, E., Edwards, D. & Axe, L. D. (2015). The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. Neofossil 197, 264–275.

Horwath, M. C., Fischer, R. A. & Depp, G. G. Jr. (2015). Histoplasma capsulatum, lung infections and immunology. Fungal Microbiology 10, 967–975.

Hotaling, S., Hood, E. & Hamilton, T. L. (2017). Microbial ecology of mountain glacier ecosystems: biodiversities, ecological connections, and implications of a warming climate. Environmental Microbiology 19, 2935–2948.

Hood, J. D. & Underhill, D. M. (2013). Striking a balance: fungal commensalism versus pathogenesis. Current Opinion in Microbiology 16, 366–373.

Inglis, G. D. & Kawchuk, I. M. (2002). Comparative degradation of comycete, ascomycete, and basidiomycete cell walls by mycoparasitic and biocontrol fungi. Canadian Journal of Microbiology 48, 60–70.

James, T. Y., Porter, T. M. & Martin, W. W. (2014). 7 Blastocladosiomycota. In The Mycota: A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research. VII. Systematics and Evolution Part A. Springer Berlin Heidelberg, Berlin, Heidelberg.

Jeffares, D. C. (2018). The natural diversity and ecology of fission yeast. Yeast 35, 253–260.

Jeffares, P. (1995). Biology and ecology of mycoparasitism. Canadian Journal of Botany 73, 1284–1290.

Jiang, X., Xiang, M. & Liu, X. (2017). Nematode-trapping fungi. Microbiology Spectrum 5, 1–12. https://doi.org/10.1128/microbiolspec.FUNK-0002-2016.

Jiang, X., Ye, H., Xiang, M., Liu, X. & Liu, X. (2011). Echinolochrysomyces varia, a new genus and species of Zygomyctea from soil isolates. Fungal Diversity 46, 43–51.

Jiménez-Guri, E., Huerta-Cepas, J., Cozzotto, L., Wotton, K. R., Kang, H., Himmelbauer, H., Rima, G., Galadés, T. & Jaeger, J. (2013). Comparative transgenicomic studies depict genome evolution. BMC Genomics 14, 123.

Jiménez-López, M. C. & Sánchez, M. C. (2013). Fungal immune evasion in a model host-pathogen interaction: Candida albicans versus macrophages. PLoS Pathogens 9, 1–9.
Evolutionary and ecological transitions in fungi

secondary metabolite gene cluster in budding yeasts. Proceedings of the National Academy of Sciences 115, 11030–11035.

Krnas, M., Tiraldo, T. M., & Dotzler, N. (2013). Fossil evidence of the zygomycete fungus. Protist 30, 1–10.

Kubicek, C. P., Herrero-Estrada, A., Seidl-Seiboth, V., Martinez, D. A., Druzhinin, I. S., Thon, M., Zeilinger, S., Casas-Flores, S., Horwitz, B. A., Murerjee, P. K., Murerjee, M., Kredics, L., Alcaraz, L. D., Aerts, A., Antal, Z., et al. (2011). Comparative genome sequence analysis underscores mycoparasitism as the ancestral lifestyle of Trichoderma. Genome Biology 12, R10.

Kuo, Y., Kohler, A., Martin, E. M., & Grigorov, I. V. (2014). Expanding genomes of mycorrhizal symbiosis. Frontiers in Microbiology 5, 382.

Kurtzman, C. P. & Robnett, C. J. (2012). Saitaella coloradensis sp. nov., a new species of the Ascomycota, subphylum Taphrinomycotina. Antonie Van Leeuwenhoek 101, 795–802.

Kurtzman, C. P. & Sugiyama, J. (2015). 1 Saccharomycosina and Taphrinomycosina: the yeasts and yeastlike fungi of the Ascomycota. In The Mycota: A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research. VII. Systematics and Evolution Part B, Edition (eds J. J. McLaughlin and J. W. Spanu), pp. 33–35. Springer, Berlin Heidelberg.

Kwon-Chung, K. J. (1975). A new Genus, Filobasidiella, the perfect state of Cryptococcus neoformans. Mycologia 67, 1197.

Kwon-Chung, K. J. (1976). A new species of Filobasidiella, the sexual state of Cryptococcus neoformans B and C serotypes. Mycologia 68, 942.

Kwon-Chung, K. J., Fraser, J. A., Doering, T. L., Wang, Z., Janbon, G., Ionuma, A. & Bash, Y.-S. (2014). Cryptococcus neoformans and Cryptococcus gattii, the etiologic agents of cryptococcosis. Cold Spring Harb Perspect Biol 6, a019760.

Lachance, A. F., Diederich, A. & Barr, C. P. (2011). Comparative genomics and evolutionary insights into the calcium-calcineurin signaling pathway in fungal cells and their potential as antifungal targets. Eukaryotic Cell 10, 324–334.

Liu, Y. J., Hall, B. D. & Taylor, T. N. (2004). Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny. Proceedings of the National Academy of Sciences 101, 4507–4512.

Liu, Y. J., Hodson, M. C. & Hall, B. D. (2006). Loss of the flagellum happened only once in the fungal lineage: phylogenetic structure of kingdom fungi inferred from RNA polymerase II subunit genes. BMC Evolutionary Biology 6, 74.

Lofgren, I. A., LeBlanc, N. R., Certano, A. K., Nachtigall, J., Labine, K. M., Riddle, J., Broz, K., Dong, Y., Bethan, B., Kaper, C. W. & Kistler, H. C. (2010). Fissarium graminum: pathogen or endophyte of North American grasses? New Phytologist 219, 1203–1212.

Low, G. J., Despons, L., Friedrich, A., Martin, T., Durrens, P., Casaregola, S., Neuvilegge, F., Fairhead, C., Marck, C., Cruz, J. A., Straub, M.-L., Kugler, V., Sacerdot, C., Uzunov, Z., Thierry, A., et al. (2012). Pochia sobolifolia, an interspecies yeast hybrid, reveals early steps of genome resolution after polyploidization. Genes Genomes Genet 2, 299–314.

Liu, H.-L. & St. Leger, R. J. (2016). Insect immunity to entomopathogenic fungi. Advances in Genetics 94, 251–285.

Lücking, R., Dal-Forno, M., Skarodoni, M., Gilleveit, P. M., Bungartz, F., Moncada, B., Yánez-Ayavaca, A., Chaves, J. L., Cong, L. & Liwy, J. D. (2014). A single macrilocus constitutes hundreds of unrelated species. Proceedings of the National Academy of Sciences of the United States of America 111, 11091–11096.

Lücking, R., Huhnendorf, S., Pinter, D. H., Plata, E. R. & Lumbsch, H. T. (2009). Fungi evolved right on track. Mycologia 101, 810–822.

Lundell, T. K., Mäkelä, M. S. & Hillkon, A. (2010). Lignin-modifying enzymes in filamentous basidiomycetes - ecological, functional and phylogenetic review. Journal of Basic Microbiology 50, 2–20.

Luo, H., Li, X., Li, G., Pan, Y. & Zhang, K. (2006). Acanthobacillus etiologicus form novel spiny structures and infects nematode. Mycologia 98, 1216–1224.

Lutzoni, F., Nowak, M. D., Alfaro, M. E., Reeb, V., Madsen, J. K., Arnold, A. E., Lewis, L. A., Swofford, D. L., Hibbett, D., Hilu, K., James, T. Y., Quandt, D. & Magallón, S. (2010). Contemporaneous radiations of fungi and plants linked to symbiosis. Nature Communications 1, 9451.

Lutzoni, F., Page, M. & Reeb, V. (2001). Major fungal lineages are derived from lichen symbiotic ancestors. Nature 411, 937–940.

Ma, L., Chen, Z., Huang, D. W., Ketty, G., Ishihara, M., Wang, H., Abraham, E., Bishop, L., Davey, E., Deng, D., Deng, X., Fan, L., Fantoni, G., Fitzgerald, M., Gogonea, E., et al. (2016). Genome analysis of three Phaeosphaeria species reveals adaptation mechanisms to life exclusively in mammalian hosts. Nature Communications 7, 10740.

Malcolm, T. R. & Chen, H.-P. (2013). Evolutionary mycoses in mammalian compromised hosts. Current Infectious Disease Reports 15, 536–547.

de Man, T. J. B., Stajich, J. E., Kubicek, C. P., Teiling, C., Ghenthamara, K., Afanasova, L., Druzhinina, I. S., Levenkova, N., Birnbaum, S. S. L., Barrieau, S. M., Bozic, B. A., Suen, G., Currie, C. R. & Gerardo, N. M. (2016). Small genome of the fungus Escocypus werneckii, a specialized disease agent of art agriculture. Proceedings of the National Academy of Sciences of the United States of America 113, 3567–3572.

Mann, S. & Chen, Y.-P. (2010). Bacterial genomic G+C composition-eliciting environmental adaptation. Genomics 95, 7–15.

Manning, R. J. & Callaghan, A. A. (2008). Pathogenicity of Conidiobolus spp. and Batrachochytrium ranarum to arthropods co-occurring in leaf litter. Fungal Ecology 1, 33–39.

Manning, R. J., Waters, S. D. & Callaghan, A. A. (2007). Saprotrophy of Conidiobolus and Batrachochytrium in leaf litter. Mycological Research 111, 1437–1449.

Manohar, C. S., Raghukumar, C., Sumathi Manohar, C. & Raghukumar, C. (2013) Fungal diversity from various marine habitats deduced through culture-independent studies. FEBS Microbiology Letters 341, 69–78.

Marcet-Houben, M., Ballester, A.-R., de la Fuente, B., Hauke, C., Marcos, J. F., González-Candelas, L. & Gaboradín, T. (2012). Genome sequence of the necrotrophic fungus Penicillium digitatum, the main postharvest pathogen of citrus. BMC Genomics 13, 466.

Marcet-Houben, M. & Gaboradín, T. (2015). Beyond the whole-genome duplication: phylogenetic evidence for an ancient interspecies hybridization in the baker’s yeast lineage. PLoS Biology 13, 1–26.

Morad, F., Arroyo, A., Almería, D., Danchin, E. G. J., Duchateau, F., Giron, J., Kohler, A., Lindquist, E., Pereda, V., Salamov, A., Shapiro, H. J., Wuyts, J., Blaudez, D., Buée, M., et al. (2008). The genome of Lycopersicon esculentum provides insights into mycorrhizal symbiosis. Nature 452, 88–92.

BMC Genomics 13, 466.
Morin, E., Miyauchi, S., San Clemente, H., Chen, E. C., Pelin, A., de la Providencia, I., Nekumana, S., Beaudet, D., Hainaut, M., Druol, E., Kuo, A., Tang, N., Roy, S., Vila, J., Henrissat, B., et al. (2019). Comparative genomics of Blichoiella irregularis, R. cerebriforme, R. diaphanus and R. irregularis: Widespread gene losses and non-synonymous substitutions in the fungal pan-genome. Genome Biology 20, 118–123.

Morita, T., Koke, H., Haga-iwara, H., Ito, E., Machida, M., Sato, H., Abe, H., & Kitamoto, D. (2014). Genome and transcriptome analysis of the basidiomycetous yeast Pseudomyces antarctica producing extracellular glycopolysaccharides, mannosylsphingosyl lipids. Fems Yeast Research 14, e106490.

Morris, J. L., Puttick, M. N., Clark, J. W., Edwards, D., Kenrick, P., Pressel, S., Wellman, C. H., Yang, Z., Schneider, H. & Donoghue, P. C. J. (2018). The rise and fall of early land plant evolution. Proceedings of the National Academy of Sciences of the United States of America 115, 15247–15249.

Morrow, C. A. & Fraser, J. A. (2013). Ploidy variation as an adaptive mechanism in human pathogenic fungi. Sensors in Cell and Developmental Biology 24, 339–346.

Mueller, U. G. & Gerardo, N. (2002). Fungus-farming insects: multiple origins and diverse evolutionary histories. Proceedings of the National Academy of Sciences of the United States of America 99, 15247–15249.

Mueller, U. G., Gerardo, N. M., Aanen, D. K., Sext, D. L. & Schultz, T. R. (2005). The evolution of agriculture in insects. Annual Review of Ecology, Evolution, and Systematics 36, 363–395.

Mukherjee, P. K., Horvitz, B. A., Herrerra-Estrilla, A., Schmoll, M. & Kerevel, C. M. (2013). Trichoderma research in the genome era. Annual Review of Phytopathology 51, 105–129.

Muto, H., Naya, H., Zavala, A., Romero, H., Alvarez-Valin, F. & Bernardi, G. (2006). Genomic GC level, optimal growth temperature, and genome size in Pseudomonas. Biotechnical and Biochemical Engineering 72, 67–71.

Mylonakis, E., Casadevall, A. & Ausubel, F. M. (2007). Exploiting amoeboid and non-vertebrate animal model systems to study the virulence of human fungal pathogens. PLoS Pathogens 1, e1000090.

Nagahama, T., Takahashi, E., Nagano, Y., Arizel-Wahab, M. A. & Miyazaki, M. (2011). Molecular evidence that deep-branching fungi are major fungal components in deep-sea methane cold-seep sediments. Environmental Microbiology 13, 2539–2570.

Nagy, L. G., Oeh, R. A., Kovacs, G. M., Floudas, D., Riley, R., Gacer, A., Spieszki, M., Davis, J. M., Dott, S. L., de Hoog, G. S. L., Bang, B. F., Spatafora, J., Salamov, A., Martin, F. M., Griswold, J. W., & Hirubert, D. S. (2014). Large-scale genome and convergent regulatory evolution underlies the repeated emergence of yeasts. Nature Communications 5, 4471.

Naumov, G. I., Kondratieva, V. I. & Naumova, E. S. (2015). Hybrid sterility of the yeast Schizosaccharomyces pombe: genetic genus and many species in statu nascendi? Microbiology 184, 159–169.

Neaphy, D. E., Barber, B. M., Sharpson, T. J., Stajich, J. E., Park, D. J., Whiston, E., Hung, C.-Y., Mchamota, C., White, J., Sykes, S., Heiman, D., Young, S., Zheng, Q., Abouelell, A., Aptick, L., et al. (2019). Population genome sequencing of Coelomycetes fungi reveals recent hybridization and transposon control. Genome Research 20, 938–946.

Nelson, M. P., Dimichele, W. A., Peters, S. E., Boyle, C. K. & Pfeiffer, H. W. (2015). Delayed fungal evolution did not cause the Paleozoic peak in coal production. Proceedings of the National Academy of Sciences 112, 2442–2447.

Nishi, H. (2018). Schizochrome mycology: Japanese fusarium: the fusion yeast is a fusion of yeast and lyophyta. Yeast 31, 83–90.

Nilsen, T., Daniel, G., Kirk, T. K. & Ost, J. R. (1988). Chemistry and microscopy of wood decay by some higher Ascomycetes. Holzforschung 43, 11–18.

Nishino, T., Takahashi, M., Lin, C.-P., Koga, R. & Futaki, T. (2016). Fungal and bacterial endosymbionts of earthen kithoppers of the subfamily Lediniidae (Hemiptera: Cicadellidae). Applied Entomology and Zoology 51, 465–477.

Notha, H. & Kodama, K. (1996). Phylogenetic position of yeastlike endosymbionts of antherostemons. Applied and Environmental Microbiology 62, 162–167.

O’Connell, R. J., Thom, M. R., Hacquard, S., Ayotte, S. G., Kleemann, J., Torres, M. F., Damm, U., Buitae, E. A., Epstein, L., Alkan, N., Altinmoller, J., Alvarado-Balderrama, L., Bauer, C. A., Becker, C., Birren, B. W., et al. (2012). Lifestyle transitions in plant pathogen Colletotrichum fuscum deciphered by genome and transcriptome analyses. Nature Genetics 44, 1060–1063.

O’Connell, R. J. & Weinstuch, H. W. (2017). Yeast genomes. In: Prokaryotes, Microbial, chemical, and enzymatic aspects of the fungal attack on lignin. Encyclopedia of lignocellulosic materials. New Phytologist, 163, 1406–1411.

Oen, R. A., Riley, R., Salamov, A., Min, B., Choi, I.-G. & Gregory, I. V. (2014). Genomics of wood-degrading fungi. Fungal Genetics and Biology 72, 82–90.

Ökmen, B. & Doddheim, G. M. (2014). Inside plant: biotrophic strategies to modulate host immunity and metabolism. Current Opinion in Plant Biology 20, 19–25.

Ouyang, C. M. & Lüönd-de-Llaca, L. V. (2007). Fungal egg-pores of plant-parasitic nematodes from Spanish soils. Revista Iberoamericana de Fisiología Vegetal 51, 101–117.

Ouyang, C. M. & Lüönd-de-Llaca, L. V. (2007). Fungal egg-pores of plant-parasitic nematodes from Spanish soils. Revista Iberoamericana de Fisiología Vegetal 51, 101–117.
Evolution and ecological transitions in fungi

Olson, Á., Aerts, A., Asea, G., Belzhuiri, L., Bouzid, O., Broberg, A., Canad, B., Coutinho, P. M., Cullen, D., Dalmau, K., Deflorio, G., van Deenen, L. T. A., Dunand, C., Duplessis, S., Durling, M., et al. (2012). Insight into trade-off between wood decay and parasitism from the genome of a fungal endophyte. *Fungal Biology* 119, 1001–1013.

Onoře, S., Belkema, L., de Hoog, G. S., Groote, M., Barrea, D., Ruisi, S. & Zucco, L. (2007). Evolution and adaptation of fungi at boundaries of life. *Advances in Space Research* 40, 1637–1644.

Orchard, S., Hilton, S., Bending, G. D., Dickie, A., Standish, R. J., Grey, D. B. J., Gury, R. P., Powell, J. R., Walker, C., Bass, D., Mon, J., Simonin, A. & Ryan, M. H. (2017). Fine endophytes (*Glomus tenue*) are related to *Macroceromyxa*, not *Glomeromyxa*. *New Phytologist* 213, 481–486.

Ortiz-Uruquiña, A. & Keyhani, N. O. (2013). Stress response signaling and virulence: insights from entomopathogenic fungi. *Current Genetics* 61, 239–249.

Ostrowski-Veichel, L. (2012). Invasive mycoses: diagnostic challenges. *American Journal of Medicine* 125, S14–S24.

Ouleh, N., Schulz, B. J. & Carrier, T. J. (2016). English translation of Heinrich Anton de Bary’s 1875 speech ‘The Escheimer von der Symbose’. *De la Symbose*. *Symbiosis* 69, 131–139.

Paks, H. C., Tavare, A. H. F., Fernandez, L., Silva-Pereira, I. & Casadevall, A. (2013). The transcriptional response of *Cryptococcus neoformans* to ingestion by *Acanthamoeba castellanii*. *Coordinates* 61, 205–217.

Pérez-Uribe, B.D. & Carrillo, M.C. (2011). Somatic hybridization in the *Uredinales*. *Mycologia* 103, 931–941.

Read, D. J., Duckett, J. G., Francis, R., Ligrone, R. & Russell, A. (2000). Symbiotic fungal associations in ‘lower’ land plants. *Philosophical Transactions of the Royal Society of London. Series B* 355, 815–830.

Reed, J. G. (2011). *Ecology on land*. *Philosophical Transactions of the Royal Society of London. Series B* 366, 722–727.

Reéllack, J. G. & Landing, E. (2014). Affinities and architecture of Devonian trunks of *Prototaxites magnum*. *Mycolologia* 106, 1143–1158.

Revankar, S. G. & Sutton, D. A. (2010). Melanized fungi in human disease. *Clinical Microbiology Reviews* 23, 681–928.

Riccardo Criado, P., Beatriz de Oliveira, C., Cristina Dantas, K., Amaro Takiguti, F., Vanconcellos Benid, L. & Vanconcellos, C. (2011). Superficial mycosis and the immune response elements. *Brazilian Annals of Dermatology* 60, 726–731.

Richards, T. A., Jones, M. D. M., Leonard, G. & Bass, D. (2012). Marine fungi: taxonomy and molecular diversity. *Annual Review of Marine Science* 4, 495–522.

Richards, T. A., Leonard, G., Madé, F., Del Campo, J., Romac, S., Jones, M. D. M., Maguire, F., Duthorn, M., De Vargas, C., Massana, R. & Chambouvet, A. (2015). Molecular diversity and distribution of marine fungi across 130 European environmental samples. *Proceedings of the Royal Society Biological Sciences* 282, 1–10. https://doi.org/10.1098/rspb.2015.2243.

Richards, T. A., Leonard, G. & Wideman, J. G. (2017). What defines the “Kingdom” Fungi? *Microbiology Spectrum* 5, 1–21. https://doi.org/10.1128/microbiolspec.FUNK-0044-2017.

Riccardo Criado, T. A., Soanes, T. M., Foster, P. G., Leonard, G., Thornton, C. R. & Talbot, N. J. (2009). Phylogenomic analysis demonstrates a pattern of rare and ancient horizontal gene transfer between plants and fungi. *The Plant Cell* 21, 1897–1911.

Richards, T. A. & Talbot, N. J. (2013). Horizontal gene transfer in oomycetes: plant–fungus public goods. *Nature Reviews Microbiology* 11, 720–727.

Rissmann, L. & Fischl, F. (2008). Changing epidemiology of systemic fungal infections. *Clinical Microbiology and Infection* 14, 5–24.

Rissmann, L., Bauer, R., Kellner, R., Kemler, M., Peter, M., Vánky, K. & Begerow, D. (2015). Identification of a new order of root- colonising fungi in the *Eutirichomyces*: taltosomyctes ord. nov. on endocladosydons. *I & M Fungi* 6, 129–133.

Riley, R., Salamov, A. A., Brown, D. W., Napy, L. G., Floudas, D., Held, B. W., Levysseuve, A., Lombrar, V., Morin, E., Ottlair, R., Lindquist, E. A., Sun, H., Labutti, K. M., Schmutz, J., Jarrour, D., et al. (2014). Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/heterotrophic paradigm for wood decay fungi. *PNAS* 111, 9929–9928.

Rimington, W., Pressel, S., Duckett, J. G., Field, K. J., Read, D. J. & Bidartondo, M. I. (2018). Ancient plants with ancient fungi: liverworts associate with early-diverging arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B: Biological Sciences* 285, 20181600.

Rincón, J., Scarpacci, L. M., Carazzolle, M. F., Mondello, J. M. C., Formigieri, E. F., Barau, J. G., Conte, G. G. L., Carrao, D. M., Brentani, H. P., Vilas-Boas, A. L., de Oliveira, B. V., Sabia, M., Dias, R., Carreiro, J. M., Azevedo, R. A., et al. (2009). Differential gene expression between the biotrophic-like and saprotrophic mycelia of the worms’ brother pathogen *Manduclaliphius pecinosum*. *Molecular Plant-Microbe Interaction* 21, 891–908.

Riquelme, M., Aguirre, J., Bartnicki-Garcia, S., Braun, G. H., Feldbrügge, M., Fleig, U., Handschke, W., Herrera-Estrella, A., Kampfer, J., Köck, U., Moureño-Pérez, R. R., Takahata, N. & Fischer, R. (2018). Fungal morphogenesis, from the polarized growth of hyphae to complex reproduction and infection structures. *Microbiology and Molecular Biology Reviews* 82, e00068–e00017.
Miguel A. Naranjo-Ortiz and Toni Gabaldón

Riquelme, M. & Sánchez-León, E. (2014). The Spitzenkörper: a choreographer of fungal growth and morphogenesis. Current Opinion in Microbiology 20, 27–33.

Roberson, R. W., Saucedo, E., Maclean, D., Prospathi, J., Unger, B., Onelo, T. A., Parvanzhoghar, K., Cavanagh, C. & Lowry, D. (2011). The hyphal tip structure of Basidiomycota: a zygomycete fungus of uncertain phylogeny. Fungal Biology 115, 485–492.

Rodríguez, R. J., White Jr., J. F., Arnold, A. E. & Redman, R. S. (2009). Fungal endophytes: diversity and functional roles. New Phytologist 182, 314–330.

Rodríguez-Carrees, M., Findley, K., Sun, S., Dietrich, F. S. & Heitm, J. (2010). Morphology and genomic characterization of Filobasidiella depauperata, a homothallic sibling species of the pathogenic Cryptococcus species complex. PLoS One 5, e9620.

Rojas-Jimenez, 5, 13–13. 133.

Sacco, A., Vidotto, F., de Hoog, S. G. (2010). Clinical and laboratory update on blastomycosis. In C. L. G. de Hoog, L. G. Wimmer and R. P. van der Graaf, pp. 485–492.

Sandoval, A. & Sánchez-León, E. (2014). Black yeasts and their filamentous relatives: principles of pathogenesis and host defense. Clinical Microbiology Reviews 27, 327–542.

Shang, Y., Xiao, G., Zheng, P., Cen, K., Zhan, S. & Wang, C. (2016). Divergent and convergent evolution of fungal pathogenicity. Genome Biology and Evolution 8, 1, 1346–1407.

Shen, S. K. & Dowd, P. F. (1989). Xenobiotic induction of esterases in cultures of the yeast-like symbiont from the cigarette beetle. Entomologia Experimentalis et Applicata 52, 179–184.

Shen, S. K. & Dowd, P. F. (1991). Detoxification spectrum of the cigarette beetle symbiont Symbiotaphrina kochii in culture. Entomologia Experimentalis et Applicata 59, 51–59.

Shoah, S. (2013). Emerging fungal infections in solid organ transplant recipients. Infectious Disease Clinics of North America 27, 305–316.

Short, D. P. G., O’Donnell, K. & Geiser, D. M. (2014). Clonality, recognition, and hybridization in the phum-inhabiting human pathogen Fusarium keratoplasticum inferred from multisecus sequence typing. BMC Evolutionary Biology 14, 91.

Shoogil, J. C., Berrin, J. G., Bey, M., Lesage-Messen, L., Levesque, A., Lomosco, A., Record, E. & Uzan-Boukhris, E. (2012). Fungal strategies for lignin degradation. Advances in Botanical Research 61, 263–308.

Silliman, B. R. & Newell, S. Y. (2005). Fungal farming in a small. Proceedings of the National Academy of Science 100, 15643–15648.

Sillo, F., Garbelotto, M., Friedman, M., Gonthier, P., Sciences, F. & Paolo, L. (2015). Comparative genomics of sibling fungal pathogenic taxa identifies adaptive evolution without divergence in pathogenicity genes or genomic structure. Genome Biology and Evolution 7, 3190–3206.

Singh, K. P., Vais, S. S., Kumar, N., Singh, D. K. & Kumar, M. (2012). Catarina angillari as an efficient biological control agent of Agasta tritici in vitro. Biological Control 63, 185–193.

Singh, U. B., Sahu, A., Sahu, N., Singh, R. K., Singh, D. K., Singh, B. P., Vaiswal, R. K., Singh, D. P., Raj, P. J., Manan, M. C., Singh, K. P., Srivastava, J. S., Rao, S. A. & Rajendra Prasad, S. (2013). Nematophagous fungus: Catarina angillari and Dicytostelium bulgarum from seed galls as potential biocontrol agents of Aegilops and Melanocarpus micranthos in wheat (Triticum aestivum L.). Biological Control 67, 475–492.

Soszos, S., Toni, L., Ferrari, A., Ferrari, A., Tononi, P., Bellin, D., Maarhouf, M., Gesler, C., Delledonne, M. & Pertot, I. (2015). Transcriptional reprogramming of the mycoparasitic fungus Ampelomyces quisqualis during the powdery mildew host-induced germination. Phytopathology 105, 199–209.

Sipman, H. J. M. & APTHORPT, A. (2001). Where are the missing fungi? Mycological Research 105, 1433–1439.

Sipos, G., Anderson, J. B. & Nagy, L. G. (2018). Armillaria. Current Biology 28, R297–R298.

Sipos, G., Prassanna, A. N., Walter, M. C., O’Connor, E., Bãlãnt, K., Kiss, K., Hess, J., Varga, T., Sloi, R., Riley, R., Bõka, B., Rigling, D., Barry, K., Lee, J., et al. (2017). Genome expansion and lineage-specific genetic innovations in the forest pathogenic fungus Armillaria. Nature Ecology & Evolution 1, 193–1941.

Smick, J., Schmit, A., Foster, R., Littman, S., Kuppers, M. M. & Foreman, C. M. (2016). Biofilms on glacial surfaces: hotspots for biological activity. Biofilms and Microbiomes 2, 16008.

Spatafora, J. W., Aime, M. C., Grigoriev, I. V., Martin, F., Stajich, J. E. & Blackwell, M. (2017). The fungal tree of life: from molecular systematics to genome-scale phylogenies. Microbiology Spectrum 5, 31–34.

Spatafora, J. W., Sugg, G.-H. H., Sjung, J.-M., Hywel-Jones, N. L. & White, J. F. (2007). Phylogenetic evidence for an animal pathogen origin of ergot and the grass endophytes. Molecular Ecology 16, 1701–1711.

Spröhle, T., Teufel, V., Resi, P., Vandenpoll, D., Wolinski, H., Aime, M. C., Schneider, K., Stérenhember, E., Toome-Heller, M., Thor, G., Mayrhofer, H., Johannsson, B. & McCutcheon, J. P. (2016). Basidiomycte yeast in the cortex of ascomycete macrolichens. Science 353, 488–492.

Srikanta, D., Santiago-Tirado, F. H. & Doering, T. L. (2014). Cryptococcus neoformans: historical curiosity to modern pathogen. Folia 31, 47–60.

Srivivasan, S., Vargas, M. M. & Roberson, R. W. (1996). Functional, organizational, and biochemical analysis of actin in hyphal tip cells of Fusarium. Current Biology 6, 1–15. https://doi.org/10.1128/microbiolspec.FUNK-0055-2017.

Steinberg, G. (2007). Hyphal growth: a tale of motors, lipids, and the spinerkörper. Entomological Society 6, 351–360.

Steinberg, G., Peñalva, M. A., Riquelme, M., Wösten, H. A. & Harris, S. D. (2017). Cell biology of hyphal growth. In The Fungal Kingdom, 1st Edition (eds J. Heitman, B. J. Howlett, P. W. Crous, E. H. Stukenbrock, T. Y. James and N. A. R. Gow), pp. 185–193.

Stevenson, P. & Krumbein, W. E. (1995). Multiple stress factors affecting growth of rock-inhabiting black fungi. Botanica Acta 108, 490–496.
Evolutionary and ecological transitions in fungi

Sterling, K., Lopande, K., Pandey, R. V., Blatt, B. & Kriegner, A. (2014). Nothing special in the specialist? Draft genome sequence of Cryptosporidium antarcticus, the most extremophile fungus from Antarctica. PLoS One 9, e109088.

Sterk, G. A. (2014). Methods of discovery and techniques to study endophytic fungi producing food-related hydrocarbons. New Phytologist 203, 964–979.

Stevenuckur, E. H. (2016). The role of hybridization in the evolution and emergence of new fungal plant pathogens. Pathology 106, 104–112.

Stenius, E. G., Christiansen, F. B., Hansen, T. T., Dutcher, J. Y. & Schirmer, M. H. (2012). Fusion of two divergent fungal individuals led to the recent emergence of a unique widespread pathogen species. Proceedings of the National Academy of Sciences 109, 10551–10556.

Stürm, S. L. (2012). A history of the taxonomy and systematics of arbuscular mycorrhizal fungi belonging to the phylum Glomeromycota. Mycorrhiza 22, 247–258.

Su, H., Zhao, Y., Zhou, J., Feng, H., Jiang, D., Zheng, K.-Q. & Yang, J. (2017). Trapping devices of nematode-trapping fungi: formation, evolution, and genomic perspectives. Biological Reviews 92, 357–368.

Sugiyama, J., Hosaka, K. & Suh, S.-O. (2006). Early diverging Ascomycota: phylogenetic divergence and related evolutionary enigmas. Mycologia 98, 996–1005.

Suliman, R. F. & White, J. F. (2000). Fission glomerata as a mycoparasite of paraphyllum. Applied and Environmental Microbiology 66, 455–457.

Sun, M.-H., Gao, L., Shi, Y.-X., Li, B.-J. & Liu, X.-Z. (2006). Fungi and actinomycetes associated with Meloidogyne spp. eggs and females in China and their biocontrol potential. Journal of Invertebrate Pathology 93, 22–28.

Sun, X., Chen, W., Ivanov, S., Maclean, A. M., Wight, H., Ramakaj, T., Muday, J., Harrison, M. N. & Fei, Z. (2018). Genome and evolution of the arbuscular mycorrhizal fungus Diversitoxa epapha (formerly Glomus versiforme) and its bacterial endosymbionts. New Phytologist 211, 1556–1573.

Sun, X. & Guo, L.-D. (2012). Endophytic fungal diversity: review of traditional and molecular techniques. Mycoscience 53, 65–76.

Takehill, N. (2016). Coordinated process of polarized growth in filamentous fungi. Bioscience, Biotechnology, and Biochemistry 80, 1693–1699.

Taneja, Y., O’Donnell, K., Sarkava, M. & Sugiyama, J. (2000). Molecular phylogeny of parasitic zygomycota (Dimargaritales, zoopagales) based on nuclear small and large subunit ribosomal DNA sequences. Molecular Phylogenetics and Evolution 16, 253–262.

Tasken, M., Ucar, M. H., Unver, Y., Kara, A. A., Ozdemir, M. & Ortucu, S. (2016). Lipase production with free and immobilized cells of cold-adapted yeast Rhodotorula glutinis HL2.5. Biofuel, Lipid and Agricultural Biotechnology 8, 97–103.

Taylor, J. W. & Berbee, M. L. (2006). Dating divergences in the Fungal Tree of Life: review and new analyses. Mycologia 98, 899–949.

Taylor, J. W. & Ellison, C. E. (2010). Mushrooms: morphological complexity in the fungi. Proceedings of the National Academy of Sciences 107, 11653–11656.

Taylor, T. N. & Osbourn, J. M. (1996). The importance of fungi in shaping the paleoclimate: implications of Palaeoherbology and Palynology. Mycolological Research 99, 249–262.

Teskeredzic, L., Bahram, M., Pöhl, S., Köjlag, U., Yorou, N. S., Wisjesdunder, R., Ruz, I., Vas-Palacios, A., Thu, P. P., Suja, A., Smith, M. E., Sharg, C., Salvee, E., Sattia, A., Rosas, M., et al. (2014). Global diversity and geography of soil fungi. Science 346, 1256688.

Tesla, J., Rahmah, M., Puskepp, R. & Nilsen, R. H. & James, T. Y. (2017). Novel soil-inhabiting clades fill gaps in the fungal tree of life. Microbiology 163, 3–32.

Teskeredzic, L., May, T. W. & Smith, M. E. (2010). Ecocorallinorych fungal in fungi: global distribution, diversity, and evolution of phyllogenetic lineages. Mycologia 102, 217–263.

Thornley, M. M., Moreno, I. F., Stellos, B. J., Musznicka, A., Hainaut, M., Gonzaga, L., Abouelhile, A., Patane, J. S. L., Priest, M., Souza, R., Young, S., Fereira, K. S., Zenz, Q., da Cunha, M. M. L., Gladis, A., et al. (2017). Exploring the genomic diversity of black yeasts and relatives (Cheatothiomyce, Ascomycota). Studies in Mycology 86, 1–26.

Tixier, A., Decelle, P., Pérez, N., Cristina, F., Marañón, A., Rossi, A. & Martinez-Rossi, N. M. (2010). Dermatomycoses: host-pathogen interaction and antifungal resistance. Annales de Dermatologie et Venereologie 38, 657–667.

Tikka, J. & Lätte, J. P. (2005). Aspergillus fumigatus: saprophyte or pathogen? Current Opinion in Microbiology 8, 383–392.

Theriot, M., Dück, M. & Rempel, C. (2010). Fate of lignins in soils: a review. Applied Soil Ecology 44, 10452–10457.

Vázquez, K., Bauer, R. & Bejerow, D. (2007). Tuberomyces, a new genus for Entorrhiza calospora (Basiomycota). Mycological Progress 6, 11–14.

Vargas, M. A., Aronson, J. M. & Roberson, R. (1993). The cytoplasmic organization of hyphal tip cells in the fungus Alphomyces macrosporus. Protistologia 176, 45–72.

Velasco, E., Posada, F., Catherine Aimé, M., Pava-Ripoll, M., Infante, E. & Rehner, S. A. (2008). Entomopathogenic fungal endophytes. Biological Control 46, 72–82.

Velgraki, A., Caparcha, C., Gaianis, G., Iattra, A. & Boekhout, T. (2015). Malassezia infections in humans and animals: pathophysiology, detection, and treatment. PLoS Pathogens 11, e1004522.

Vencenc, V. A., Orello-Ribeiro, R., Najafzadeh, M. J., Sun, J., Juerga, R. S., Miesch, S., Ostrenskaya, A., Meis, J. F., Claassen, H. C., de Hoog, G. S. & Boerger, W. A. (2012). Black yeast-like fungi associated with Lethargic Crab Disease (LCD) in the mangrove-land crab, Ucides cordatus (Crustacea). Veterinary Microbiology 158, 169–172.

Vidal-Diez de Ulzurrun, G. & Hushe, Y.-P. (2018). Predator-prey interactions of nematode-trapping fungi and nematodes: both sides of the coin. Applied Microbiology and Biotechnology 102, 1–11.

Vlaardingerbroek, I., Beeren, B., Rose, L., Forkens, L., Cornelissen, B. J. C. & Rep, M. (2016): Exchange of core chromosomes and horizontal transfer of lineage-specific chromosomes in Fusarium oxysporum. Environmental Microbiology 18, 3702–3713.

Voglmayr, H., Mayer, V., Marschitz, U., Moog, J., Dijetro-Lordon, C. & Blatrix, R. (2011). The diversity of ant-associated black yeasts: insights into a new ant-protected world of fungal endophytes. New Phytologist 195, 1077–1091.

Voyo, L., Rosenblum, E. B. & Berger, L. (2011). Interactions between Batrachochytrium dendrobatidis and its amphibian hosts: a review of pathogenesis and immunity. Microbes and Infection 13, 25–32.

Vujanovic, V. & Kim, S. H. (2017). Adaptability of mitoposite stage in Stachybotrys auralicola towards its mycoparasitic-polyphagous lifestyle. Mycologia 109, 701–709.

Wang, C. & Wang, S. (2017). Insect pathogenic fungi: genomics, molecular interactions, and genetic improvements. Annual Review of Entomology 62, 73–90.
Whiston, Biological Reviews 94 (2019) 1433–1476

Miguel A. Naranjo-Ortiz and Toni Gabaldón

Wang, Q.-M., Begerow, D., Groenewald, M., Liu, X.-Z., Theelen, B., Bai, F.-Y. & Boekhout, T. (2013). Multigene phylogeny and taxonomic resolution of yeasts and related fungi in the Ustilaginomycotina. *Studies in Mycology* 81, 53–83.

Wang, Q.-M., Yurkov, A. M., Göker, M., Lumbsch, H. T., Leavitt, S. D., Groenewald, M., Theelen, B., Liu, X.-Z., Boekhout, T. & Halfferty, V. (2015). Phylogenetic classification of yeasts and related taxa within Pucciniozymata. *Studies in Mycology* 81, 149–189.

Wang, X., Jiang, N., Liu, J., Liu, W. & Wang, G.-L. (2014). The role of effectors and host immunity in plant-nectrotrophic fungal interactions. *Nature Genetics* 46, 1–10.

Wang, Y.-Y., Liu, B., Zhang, X.-Y., Zhou, Q.-M., Zhang, T., Li, H., Yu, Y.-F., Zhang, X.-L., Hao, X.-Y., Wang, M., Wang, L. & Wei, J.-C. (2014). Genome characteristics reveal the impact of lichenization on lichen-forming fungus *Endocarpon lasiospermum* Hedwig (Verneucciariaceae, Ascomycota). *R&H* 15, 1–18. https://doi.org/10.1186/1747-1252-15-34.

Wang, Z. K., Yang, Y. S., Steeke, A. T., Sun, G. & Peng, L. H. (2014). Review article: fungal microbiota and digestive diseases. *Alimentary Pharmacology and Therapeutics* 39, 751–766.

Wani, A., Ashraf, N., Mohiuddin, T. & Riaz-Ul-Hassan, S. (2015). Plant-endophyte symbiosis, an ecological perspective. *Apllied Microbiology and Biotechnology* 99, 2953–2965.

Warnock, D. W. (2007). Trends in the epidemiology of invasive fungal infections. *Japanese Journal of Medical Mycology* 48, 1–12.

Wachter, S. A., Bezzerra, A. G., Shi, L., Brown, L. S. & Brown, L. S. (2005). *Leptosphaeria choduspis*: bacteriorhodopsin-like proton pump from a caryophyllaceae. *Proceedings of the National Academy of Sciences of the United States of America* 102, 6789–6793 National Academy of Sciences.

Wedin, M., Döring, H. & Giletnam, G. (2004). Saprophytic and lichenization as options for the same fungal species on different substrata: environmental plasticity or host specificity? *Ecology* 85, 722–732.

Whiston, E. & Taylor, J. W. (2014). Genomics in Cocccidioides: insights into evolution, ecology, and pathogenesis. *Medical Mycology* 52, 149–155.

White, T. C., Findey, K., Dawson, T. L., Scheunius, A., Boekhout, T., Cúneo, C. A., Xu, J., Saunders, W. & Saunders, C. W. (2014). Fungi on the skin: dermatophytes and Malassezia. *Cold Spring Harbor Perspectives in Medicine* 4, a019802.

Wiberg, D., Jelonek, L., Rupp, O., Hennig, M., Eismeyer, F., Goessmann, A., Hartmann, A., Borrens, R., Grosch, R., Pühler, A. & Schüler, A. (2013). Establishment and interpretation of the genome sequence of the phytopathogenic fungus *Rhizoctonia solani* AG1-IB isolate 73/14. *Journal of Bacteriology* 197, 142–155.

Wicker, T., Oberhaensl, S., Parlane, F., Buchmann, J. P., Shatalina, M., Roffler, S., Ben-David, R., Doležel, J., Simková, H., Schulze-Lefert, P., Spanu, P. D., Bruggmann, R., Asseleme, J., Queensville, H., Ver Loren van Themaat, R., et al. (2013). The wheat powdery mildew genome shows the unique evolution of an obligate biotroph. *Nature Genetics* 45, 1092–1098.

Wolfe, K. H. & Shields, D. C. (1997). Molecular evidence for an ancient duplication of the entire yeast genome. *Science* 270, 708–713.

Wollenberg, T. & Schierwater, J. (2014). Comparative genomes of plant fungal pathogens: the Ustilago-Sporisorium paradigm. *PLoS Pathogens* 10, e1004218.

(Received 16 October 2018; revised 10 March 2019; accepted 13 March 2019; published online 25 April 2019)