# Fungal evolution: major ecological adaptations and evolutionary transitions

Miguel A. Naranjo-Ortiz[1] and Toni Gabaldón[1,2,3]*

[1] *Department of Genomics and Bioinformatics, Centre for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology, Dr. Aiguader 88, Barcelona 08003, Spain*
[2] *Department of Experimental and Health Sciences, Universitat Pompeu Fabra (UPF), 08003 Barcelona, Spain*
[3] *ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain*

## 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 terrestralization 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

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\* 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 (Lilleskov *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 eukaryvorous parasitoids 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 Nucleariida, 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

bodies. Marine fungi do exist, but even zoosporic lineages seem to be much more diverse in non-marine environments (Richards *et al.,* 2012, 2015; Manohar *et al.,* 2013; Rämä *et al.,* 2017). Ancestral fungi must have been primarily aquatic, however, as all terrestrial fungi form a clearly monophyletic clade with a single inferred loss of the flagellum (Liu, Hodson & Hall, 2006). Thus, either Fungi originated in continental water bodies, or we are missing key marine lineages. The early-branching lineages Aphelida, Rozellida and Chytridiomycota seem to show high diversity in marine environments, based on environmental studies (Richards *et al.,* 2015; Gleason *et al.,* 2017; Tedersoo *et al.,* 2017), and some highly diverse marine chytrid lineages seem to be among the earliest to diverge, suggesting that we might be close to finding a missing link (Nagahama *et al.,* 2011; Richards *et al.,* 2015; Seto, Kagami & Degawa, 2017). Nevertheless, caution is required, as chytrid phylogeny and its positioning within the fungal tree of life remains poorly resolved.

Ecologically speaking, the parasitoid lifestyle unites the Opisthosporidia, Chytridiomycota and Blastocladiomycota; although other lifestyles are known for these groups (Fig. 1). This suggests that the ancestor of all fungi was probably a parasitoid of microalgae, with phagotrophic capabilities, showed both amoeboid and flagellar motility, and possessed chitin cell walls, at least in some life stages (Richards, Leonard & Wideman, 2017; Spatafora *et al.,* 2017). These characteristics are similar to modern Aphelidea, with *Rozella* and many chytrids sharing most of these traits, too. This suite of adaptations separates Fungi from the remaining Holomycota clades (Nucleariida and Fonticulida), that are amoeboid free-living predatory protists. This important division provides ancestral phenotypic qualities to define the fungal kingdom, which is otherwise devoid of unifying traits (Richards, Leonard & Wideman, 2017). Under this premise, early Aphelidea and Rozellida probably associated with diverse groups of algae and protozoans, whereas the ancestors of the other contemporaneous lineages likely lived mostly as parasitoids of Chlorophyta. This latter association likely involved the development of the carbohydrate active enzyme (CAZy) repertoire that characterizes most fungal lineages, as well as the development of rhizoids as penetration and anchorage structures (Lücking *et al.,* 2009; Chang *et al.,* 2015). The ability to penetrate solid surfaces and to digest cellulose and other biopolymers facilitated a lifestyle switch from parasitism to saprotrophy. Organisms with parasitoid lifestyles are rarely present at high densities in the environment, making their preservation in the fossil record less likely. However, indirect evidence of neoproterozoic eukaryovory, compatible with the activity of zoosporic fungal parasitoids, has been found (Porter, 2016). Such predatory behaviour is also known from other eukaryotes, such as vampyrellid amoebae, foraminferans and cercozoans (Porter, 2016). Future comparative genomic analyses between zoosporic fungi and their amoeboid sister lineages are likely to provide new insights on this period of fungal evolution.

## III. DOWN TO EARTH: TERRESTRIALIZATION IN FUNGI

The most definitory 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 $Ca^{2+}$ is too low to constitute a reliable source. Specialized $Ca^{2+}$ 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 $Ca^{2+}$ 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, Blastocladiella*) also have a morphologically recognizable SPK (Vargas, Aronson & Roberson, 1993; Srinivasan, Vargas & Roberson, 1996;
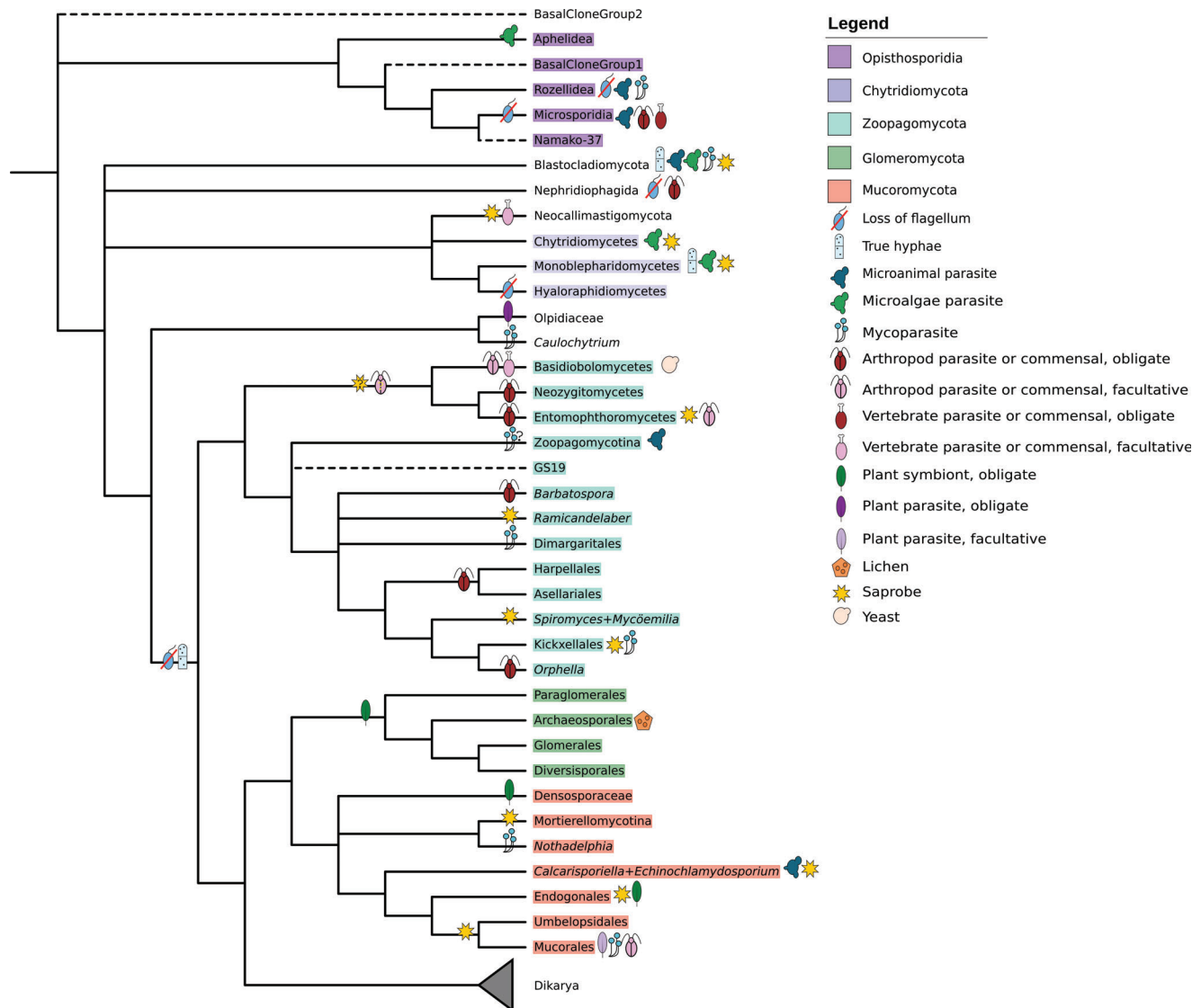
**Fig. 1.** Phylogenetic tree showing main ecological transitions across the non-Dikarya fungi. Symbols on the right indicate that the transition has occurred within the group.

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
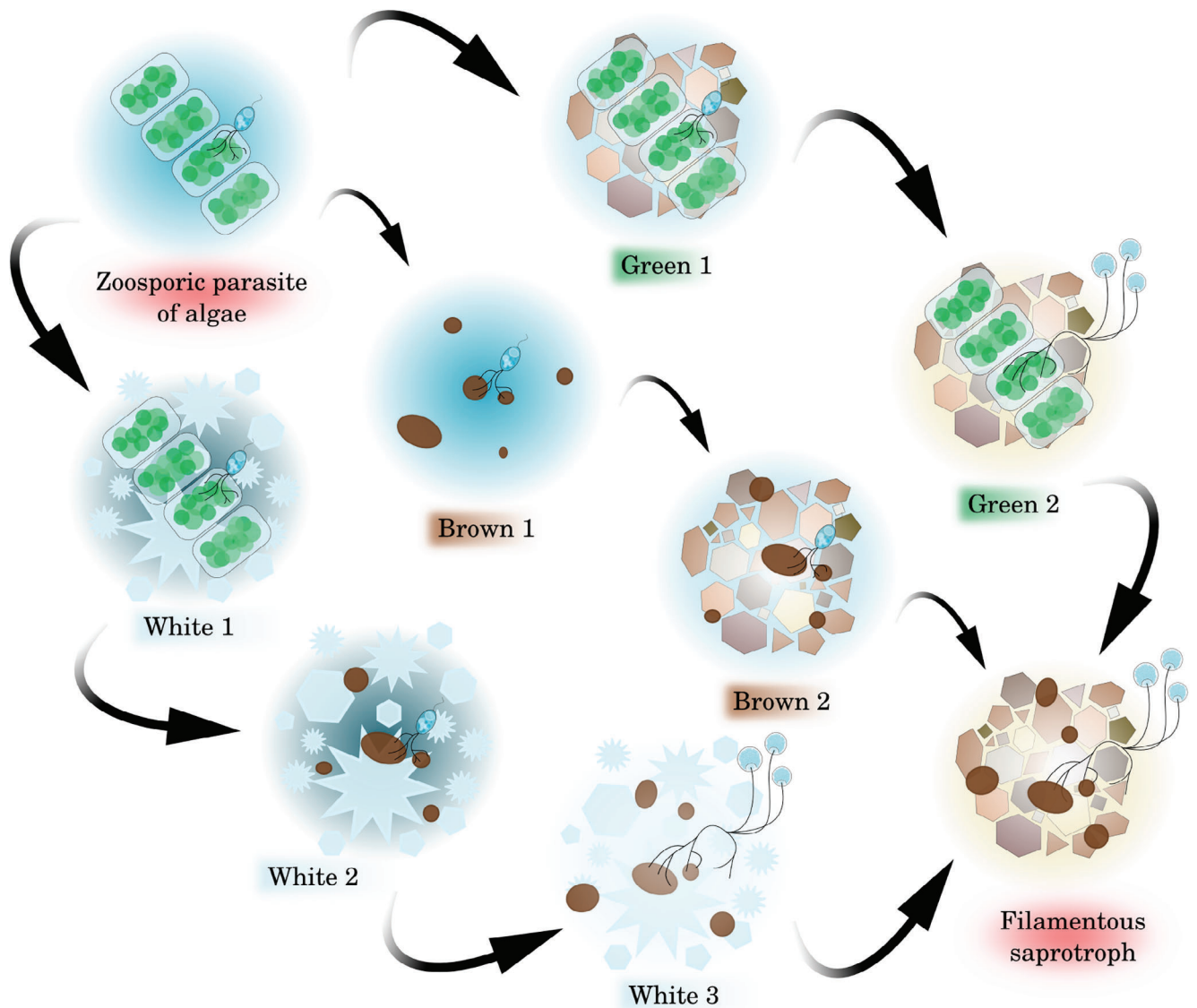
**Fig. 2.** Schematic representation of the three hypothesis for fungal terrestrialization. The 'green' scenario implies that terrestrialization of fungi was dependent on terrestrialization in green plants, probably Streptophyta. The 'brown' scenario assumes that zoosporic fungi acquired saprotrophic 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 amoebophagous 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 &

Gerdes, 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 microniches 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 microniches 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 (Kaštovská *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 periglaciar soils or arctic seas, contain an unsuspected abundance and diversity of zoosporic lineages (Freeman *et al.,* 2009; Hassett & Gradinger, 2016; Rämä *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 yeast forms of both Ascomycota and Basidiomycota (Coleine *et al.,* 2018).

Finally, the estimated dates of radiation of fungal terrestrial lineages (Taylor & Berbee, 2006; Berbee & Taylor, 2010; Prieto *et al.,* 2013*b*; Knoll, 2014; Lutzoni *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 (Trebouxiophyceae and Trentepohliales) (Lutzoni *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 microniches 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 Zoopagomycota being primarily associated with other microbes and metazoans, and the clade Glomeromycota + Mucoromycota + 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
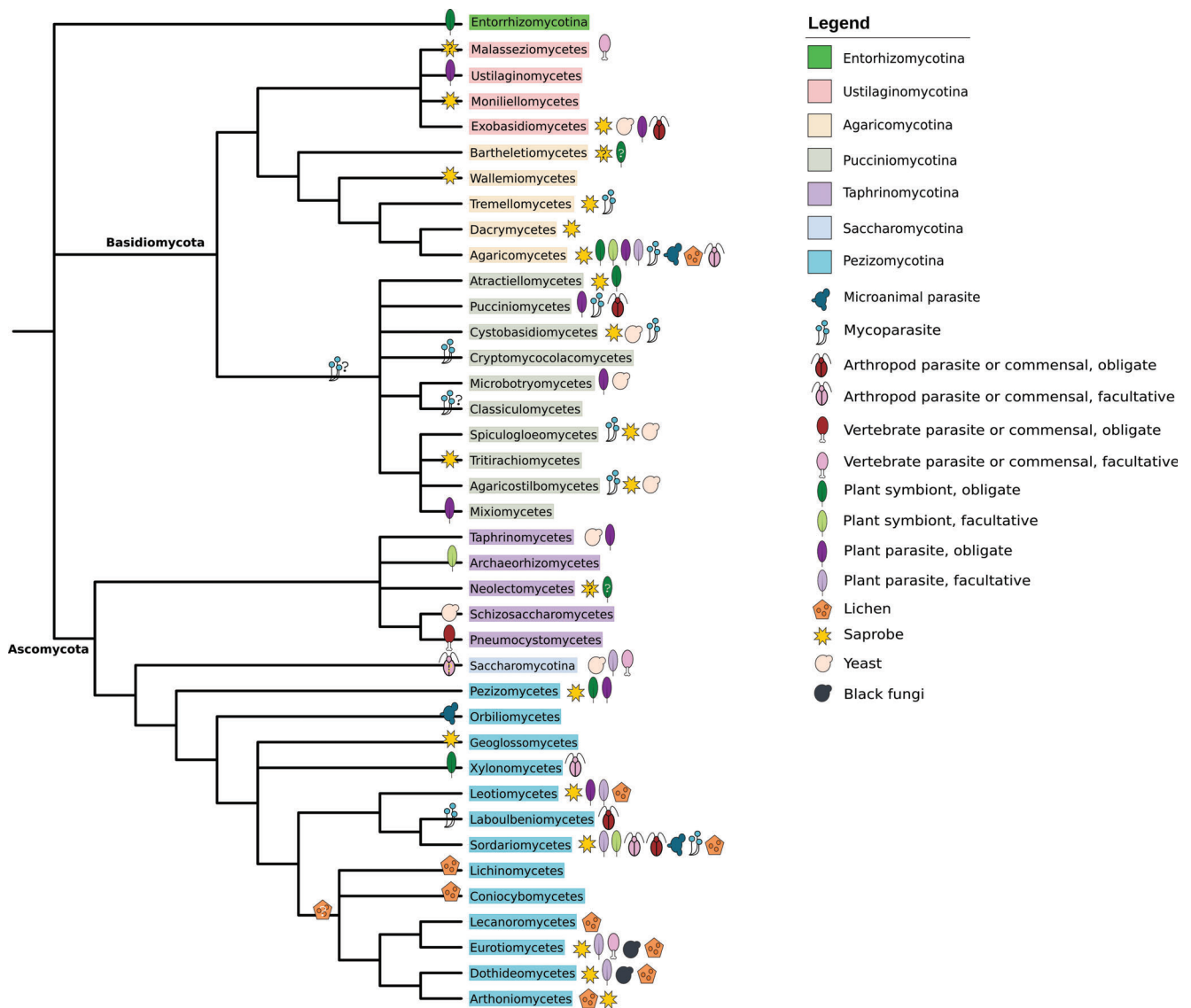
**Fig. 3.** Phylogenetic tree showing main ecological transitions across the Dikarya fungi. Symbols on the right indicate that the transition has occurred within the group.

fungi (Jeffries, 1995). 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 Sigmoideomycetaceae within the Zoopagomycotina, as well as the Dimargaritales 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

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* (Laboulbeniomycetes) (Blackwell, 1994; Kirschner, 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 *Tolypocladium* (Quandt, Bushley & Spatafora, 2015), *Clonostachys* (Karlsson *et al.*, 2015) and *Escovopsis* (de Man *et al.*, 2016). Genome comparisons of these mycoparasites show that mycotrophism 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, *Ampelomyces* (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 *Ampelomyces*. 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 *Parasitella* (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

**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 (Silliman & 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

specialized adaptations to invade the animal host, although they can be found as free-living organisms in the environment or as asymptomatic commensals in the host. We include in this category non-obligate trapping fungi, 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.*, 2014*b,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 microsporidians 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, Microsporidia 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 Microsporidia, this is a very plausible scenario.

Zoopagomycota also comprises many obligate parasites of metazoans, specially 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 (Gryganskyi *et al.*, 2013) (Fig. 4). Given that traditional filamentous growth and saprotrophy can also be found in Kickxellomycotina 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 (Gryganskyi *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 Kickxellomycotina, 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 Pezizomycotina 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 *Pyxidiophora*, 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 lifestyle (Haelewaters *et al.*, 2015; Goldmann & Weir, 2018). Finally, the genera *Septobasidium* and *Uredinella* (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 *Fibularhizoctonia* (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 Entomophthoromycotina are able to parasitize insects to some degree. *Conidiobolus* 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, *Sporodiniella umbellata* (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), Entomophthoromycotina (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; Eapen, 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 motile 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* (Burdsall, 1969; Hallenberg, 1990), acanthocytes in *Stropharia* (Luo *et al.,* 2006), or appendages in *Nematoctonus, 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 microniches. 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. salamandrivorans* (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, Terribile & Brito, 2014; Leopardi, Blake & Puechmaille, 2015). This highly virulent strain arrived from Europe, where the native bat populations are resistant to it (Leopardi, Blake & Puechmaille, 2015). The fungus is actually psychrophylic, 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-Ramírez *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 threat-ening, 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; Seyed-mousavi *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-fungi-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 & Deepe, 2015), *Blastomyces* (Saccente & Woods, 2010; Bariola & Vyas, 2011; López-Martínez & Méndez-Tovar, 2012; Malcolm & Chin-Hong, 2013; Castillo, Kauffman & Miceli, 2016), *Coccidioides* (Neafsey *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 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-Ortíz & 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; Herkert *et al.*, 2017). The fungus presents a mutinucleated and highly polyploid 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 Pezizomyctina (*Aspergillus*, *Penicillium*, *Paecillomyces*, *Acremonium*, *Fusarium*, *Trichoderma*, *Sporothrix*, *Scedosporium*), Pucciniomycotina (*Rhodotorula*), Mucoromycotina (*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-Flörl, 2008; Miceli & Lee, 2011; Shoham, 2013; Crabol & Lortholary, 2014). These fungi are usually air- and soil-borne saprotrophs 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, lipidases, 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; Kijpornyongpan *et al.*, 2019), as well as in vertebrate mucosae (Iliev & Underhill, 2013; Wang *et al.*, 2014*d*; 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 *Suhomyces* (syn. *Saccharomyces tanzawaensis*) seem to be found preferentially in such niches (Kijpornyongpan *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 (Tedersoo, 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; Hardoim *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; Hardoim *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; Hardoim *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; Kembel & 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; Tedersoo, 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 Rhynie 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 mycorrizal 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 (Sathiyadash *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 intrarradices*). 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; Hardoim *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 clavicipitcaeous and non-clavicipitaceaous (Rodriguez *et al.,* 2009; Porras-Alfaro & Bayman, 2011; Hardoim *et al.,* 2015). Many endophytes occupy other ecological niches, acting as parasites, saprotrophs or epiphytes (Rodriguez *et al.,* 2009; Rai & Agarkar, 2014; Hardoim *et al.,* 2015) (Fig. 4). Epiphytic communities include fungi and bacteria living on the surface of leaves and other parts of plants (Hardoim *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 (Santamaría & 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): Entorrhizomycota, Archaeorhizomycetes (Taphrinomycotina), some Pezizomycetes (Pezizomycotina) and probably Neolectomycetes (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. Moss 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), Archaeorizomycetes (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 archetypical 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 allow 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.*, 2014*a*). 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.*, 2014*a*; 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; Julca *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 (Pucciniomycotina, Ustilaginomycotina). Necrotrophs 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. *Rhizoctonia 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 multicelullar 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 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; Ökmen & 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.*, 2015*a*). 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, 2015). 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; Stukenbrock *et al.*, 2012; Depotter *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 are highly stable, largely insoluble and mechanically strong (Martínez *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 fully has evolved only once in the biosphere, within the class Agaricomycetes (Dashtban *et al.*, 2010; Lundell, Mäkelä & 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; Worrall, 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 (Martínez *et al.*, 2005; Lundell, Mäkelä & 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 (Karatygin, 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). *Winfrenatia reticulata* is a fossil from the Early Devonian that has been interpreted as a zygomycetous lichen (Karatygin, 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 & Gilenstam, 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, 2009). 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 eurotiomycete *Endocarpon pusillum* revealed several traits putatively related to symbiosis (Wang *et al.,* 2014b). 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).

## VIII. BLACK FUNGI

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 (Gostinčar *et al.,* 2012; Selbmann *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 are often able to exploit extremely resilient nutrient sources (Selbmann *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; Zupančič *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; Selbmann *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 (Voglmayr *et al.*, 2011).

The main unifying characteristic of black fungi is the accumulation of melanins, a generic term used to describe a diverse set of natural pigments. Melanins act as powerful protectors against oxidative damage, ionizing radiation and other damaging chemical and physical conditions. Black fungi bind melanins to their bio-molecules, particularly their cell walls, in ways that are not fully understood. Apart from melanins, these fungi tend to accumulate soluble compounds that provide protection, such as mycosporines, trehalose, polyalcohols, betaine, proline and diverse carotenoid pigments (Gorbushina, Kotlova & 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; García-Martínez *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 as yet 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 $CO_2$ 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 typical for Pezizomycotina, but they often have a very high GC content (Teixeira *et al.*, 2017; Moreno, Vicente & de Hoog, 2018). A high GC content is a common feature in extremophilic prokaryotes as it helps to stabilize DNA against physicochemical disruption (Musto *et al.*, 2006; Mann & Chen, 2010). Gene expansions are common and tend to affect genes related to transport, reactive oxygen protection, cytochromes and metabolism of unusual carbon sources. In turn, this makes the proteome of some of these fungi quite large. For example, the reference genome of the endolythic antarctic fungus *Rachicladosporium* sp. CCFEE 5018 (Capnodiales) (Coleine *et al.*, 2017) contains around 18000 genes. *Hortaea werneckii* (Capnodiales) is a highly halotolerant black fungus capable of growth at near salt-saturation conditions. *H. werneckii*, with almost 15500 protein-coding genes, underwent a recent whole-genome duplication that expanded many functions related to ion pumps and channels (Lenassi *et al.*, 2013). Whole-genome duplication might be an important evolutionary step allowing adaptation to highly specialized extreme niches, although to date *Hortaea* remains the only described example. One of the first comparative studies of black fungi involved the sequencing of the psychrophylic *Cryomyces antarcticus* (Dothideomycetes *incertae sedis*) (Sterflinger *et al.*, 2014). They compared *C. antarcticus* with several species of black fungi isolated from diverse environments. The analysis suggested that the genome of *C. antarcticus* is very similar in size, content and composition to the other black fungi considered. These results imply that either all 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 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 Chaetothryriales 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 affiliation 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 (Voglmayr *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 cluster identified very recently in *Saccharomyces* (Krause *et al.*, 2018). They usually live in association with low water 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 *Schizangiella* (Basidiobolomycetes) (Benny, Humber & Voigt, 2014), a poorly known fungus identified as a commensal in the gut of some reptiles (Fig. 1). Several clades traditionally considered as yeasts are now known to have filamentous stages in their natural environment. The genus *Cryptococcus* (Tremellomycetes) grows within a human host as a yeast, but is found in the environment growing as a filamentous mycoparasite that requires a fungal host to complete its sexual cycle. Similarly, the genus *Malassezia* (Malasseziomycetes) is a lipophillic dimorphic fungus that is traditionally associated with animal surfaces, but seems to be very common in marine environments.

Saccharomycotina is by far the most diverse and best-studied group of yeast fungi, due to their small and compact genomes, the use of *Saccharomyces cerevisiae* as a model organism, the use of several yeast species in industrial fermentation, and the health costs of some species. Members of the Saccharomycotina show a clear tendency towards genome compaction, which implies increased gene density and intron reduction (Dujon *et al.*, 2004; Dujon, 2010, 2015; Hittinger *et al.*, 2015; Dujon & Louis, 2017). Four main genomic architectures within the group can be differentiated: the early-diverging clades, the methylotrophic clades, the 'CTG' clade and the Saccharomycetaceae. Early-diverging lineages within the subphylum have compact and reduced genomes compared to Pezizomycotina. The paradigm of this heterogeneous group has traditionally been *Yarrowia lipolytica*, which has a genome of 20.5 Mbp of which 46% is coding. Its genome contains approximately 6600 genes, of which 14% contain introns. There is considerable variability within these basal lineages, with some species showing highly compact genomes (e.g. *Blastobotrys adeninivorans*), smaller genomes (e.g. *Nadsonia fulvescens*) or high intron density (e.g. *Geotrichum candidum*). There is an evolutionary tendency towards genome reduction and compaction, with the methylotrophic and CTG clades displaying intermediate levels, and reaching a maximum within the Saccharomycetaceae (Dujon *et al.*, 2004; Dujon, 2010, 2015; Hittinger *et al.*, 2015; Dujon & Louis, 2017). This group has genomes ranging from 9 to 14 Mbp with a coding density between 65 and 75%. The typical genome contains around 4500–5900 genes of which 3–5% have introns. They also manifest other exclusive genomic peculiarities related to genome compaction, such as the presence of point centromeres and a reduction of rRNA genes to a single compacted locus. It is important to note that the Saccharomycetaceae underwent a whole-genome duplication, which has had relatively little effect on their genome size (Wolfe & Shields, 1997; Marcet-Houben & Gabaldón, 2015). The ecology of this group is very diverse. In addition to species associated with sugary substrates (Pozo, Herrera & Bazaga, 2011; Lievens *et al.*, 2015), members of the Saccharomycetaceae have been found 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 *et al.*, 2007; 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 (Dodgson *et al.*,

2009, 2010; Niki, 2014). *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 *Protomyces* 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, Spiculogloeomycetes, Agaricostylbomycetes and Cystobasidiomycetes) (Aime, Toome & McLaughlin, 2014; Wang *et al.*, 2015*b* ; 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 Cryptomycocolacomycetes, 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 Saccharomycotina (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 cellulolytic capabilities. 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 paraphyletic (Aime, Toome & McLaughlin, 2014; Oberwinkler, 2017). The genomes of several red yeasts are available. The typical genome size is around 20 Mpb, with 5500–7000 protein-coding genes and typically a very high GC content. Their coding density and genome size are similar to early-branching Saccharomycotina, such as *Yarrowia*, 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 Pucciniomycotina (Wang *et al.*, 2015*b*; Oberwinkler, 2017) and Ustilaginomycotina (Wang *et al.*, 2015*a*; Kijpornyongpan *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; Lievens *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 & Plemenitaš, 2009). Yeasts, particularly from the Basidiomycota, are also common in frozen environments (Arendrup, 2013; Selbmann *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 Saccharomycetaceae. 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 Opisthosporidia, 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 Dothideomycetes and Eurotiomycetes that are able to proliferate in very hostile environments. Some of these traits are shared with lichen-forming fungi, and the two ecotypes 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

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