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Review

Fungal diversity from communities to genes

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ABSTRACT

Fungi are hyperdiverse organisms and assemble in complex communities, characterized by high levels of species richness, turnover, and endemism. However, the origins and maintenance of such high diversity and the role environments play in fungal adaptation are still elusive. Traditionally, efforts to understand fungal diversity in their environment have been divided between studies at the species level and below species level, with separate disciplines such as community ecology and population genetics working independently and with little communication. Here I argue that linking these different approaches is required to fully document the diversity of fungi in nature. Understanding the patterns and mechanisms of fungal diversity and composition requires not only the study of species assemblies and ranges, but also relies on comprehending fungal intraspecific variation, dispersal and establishment, including identifying key traits influencing fitness. This implies better integration and cross-fertilization between disciplines addressing fungi at a multitude of biological levels, ranging from genes to whole communities. Such approach will yield direct links between variation, adaptation and environments and provide a much more comprehensive understanding of fungal diversity.

1. Introduction

Fungi are remarkably diverse, with latest estimates pointing to up to 3.8 million fungal species in nature (Hawksworth and Lücking, 2017). These organisms assemble in highly diverse communities, with high levels of species richness and species turnover (Branco, 2011) and considerable endemism (Taylor *et al.*, 2006, Meiser *et al.*, 2013, Talbot *et al.*, 2014). Despite the recent advances enabled by improved sequencing technologies, full understanding of the processes and mechanisms that shape the origins and maintenance of fungal diversity in the context of environments is still lacking.

There have been two main approaches to studying fungal diversity in the environment: documenting species richness and composition (community ecology) and determining below species level diversity (population genetics and demography). Community ecology deals with investigating the distribution, structure, abundance, and interactions between species. It however ignores the existence of intraspecific variation and evolution (Mittelbach and Schemske, 2015), considering species constant and immutable entities. Population genetics focuses on the sources of intraspecific genetic variation and how natural selection shapes variation. Population genetics and adaptation studies recognize intraspecific variation, but very often disregard complex biotic contexts and species

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interactions (Exposito-Alonso *et al.*, 2017). Traditionally there has been very little communication between community ecology and population genetics, which is unfortunate since species encompass variation that determines phenotypes and physiological limits leading to differential ecological niches. In addition, biotic interactions can directly impact fitness and shape the ecology and evolution of species. Linking above- and -below species approaches is therefore necessary for a full understanding of the origins and maintenance of fungal diversity.

Shifting the focus of fungal diversity studies to include adaptive processes and outcomes ranging from genes to communities would provide a much more complete and accurate view of why and how fungi live where they live. Adaptation is the evolutionary process whereby organisms become better able to live in their habitat and propagate their genes (Darwin, 1859, Dobzhansky, 1968). It operates through natural selection on individual phenotypes and is responsible for the amazing biological diversity observed across the globe. Adaptation stems from genetic variation that is shaped by natural selection (Williams, 1966, Charlesworth *et al.*, 2017), translating phenotypes into fitness and resulting in the fit between organisms and the environments they inhabit (Grant and Grant, 2011). Adaptation plays an important role in structuring genetic pools and affects all levels of biological diversity, from molecules (Rogers *et al.*, 2017, Saavedra *et al.*, 2018, Willot *et al.*, 2018) to individuals and populations (Ellison *et al.*, 2011, Branco *et al.*, 2017, Exposito-Alonso *et al.*, 2017, Donihue *et al.*, 2018) and whole ecological communities (Mittelbach and Schemske, 2015).

Adaptation usually begins with the evolution of advantageous traits in local populations (Williams, 1966) leading local resident genotypes to exhibit higher fitness in their habitat compared to genotypes originated in other habitats (ecotypes, Kawecki and Ebert 2004). Local adaptation can be shaped by both biotic and abiotic factors (Savolainen *et al.*, 2013), and depending on the strength of natural selection and dispersal ability, can lead to population divergence and even to speciation (Sobel *et al.*, 2010, Nosil, 2012). Along with dispersal limitation, local adaptation plays an important role in determining species ranges and distributions, and consequently shapes ecological community assemblies at local, regional, and continental scales (Fig. 1).

Adaptation is an important process shaping fungal species ranges and diversity (Ellison *et al.*, 2011, Branco *et al.*, 2017, Robin *et al.*, 2017, Table 1), but it is not trivial to document (Kraemer and Boynton, 2017). Individual species composing fungal communities have specific evolutionary histories that determine their ability to colonize and withstand the habitat they occupy. These include being able to colonize that habitat, which implies the ability to disperse followed by establishment under specific environmental conditions characterized by a set of biotic and abiotic factors. Fungal species encompass genetic variation that ultimately determines their dispersal ability and physiological limits, directly affecting where they occur (Taylor *et al.*, 2017). Given the high complexity of fungal communities, much research effort has been allocated into uncovering patterns of fungal community assembly through documenting site-specific species diversity and composition using molecular barcoding approaches (e.g. Branco *et al.*, 2013, Tedersoo *et al.*, 2014, Nguyen *et al.*, 2016, Linde *et al.*, 2018), though some studies aim at also linking fungal community composition to ecosystem function by for example investigating species enzymatic activities (e.g. Talbot *et al.*, 2013, Talbot *et al.*, 2014). Such approaches provide important insight on fungal species richness, composition and distributions, and offer relevant cues for understanding the mechanisms structuring fungal diversity as a whole. However, community ecology studies most often do not include investigations of the fungal biological characteristics that are at the base of their distributions (Peay *et al.*, 2016). This derives from the fact that fungi are hyper diverse and cryptic organisms, as well as challenging study objects for which there are few available measurable traits (Branco, 2011), making it extremely difficult to unveil the biological characters involved in determining patterns of fungal diversity. This said, understanding the origins and maintenance of fungal genetic diversity, how it affects trait variability, and determines species persistence and fitness is a necessary step to fully explain overall fungal diversity, composition, and distributions. Here I review the latest developments in fungal ecology, genetics, and adaptation, and point out the benefits of crossing disciplines to better understand the origins and maintenance of fungal diversity.

2. Adaptive basis of fungal community diversity

Fungal communities tend to be very diverse, displaying high species richness and turnover, and are structured by an array of ecological and evolutionary factors acting at distinct spatial scales (Peay *et al.*, 2016). Community ecology work has identified moisture (Crowther *et al.*, 2014) and nutrient resource ability (Baldrian *et al.*, 2012, Lindahl *et al.*, 2007) as the main environmental abiotic drivers for fungal diversity and composition at the habitat level. It has also become clear that priority effects (Sutherland, 1974, Drake, 1991), competition-colonization trade-offs (Tilman, 1994, Livingston *et al.*, 2012), and dispersal limitation (Gadgil, 1971) are important phenomena determining fungal community diversity. Priority effects have been identified in wood decaying fungi (Fukami *et al.*, 2010, Dickie *et al.*, 2012, Hiscox *et al.*, 2015, Leopold *et al.*, 2017), ectomycorrhizal fungi (Kennedy and Bruns, 2005, Kennedy *et al.*, 2009), arbuscular mycorrhizal fungi (Werner and Kiers, 2014) and nectar yeasts (Peay *et al.*, 2011a), with a clear effect of order of species arrival in determining community diversity and composition. There is also evidence for fungal competition-colonization trade-offs (Tedersoo *et al.*, 2008, Smith *et al.*, 2018), with species showing distinct abilities to colonize new sites and displace already established species, influencing ecological community assembly. In addition, despite producing very large amounts of propagules many fungi do not travel far, as demonstrated by observed patterns of endemism (Meiser *et al.*, 2013, Talbot *et al.*, 2014), evidence for limited ability for spores to travel over long distances (Peay and Bruns, 2014), and absence of population gene flow across regional scales (Branco *et al.*, 2015).

Even though stochasticity is likely to play a considerable role in structuring fungal communities, phenotypic traits involved in species dispersal and habitat colonization

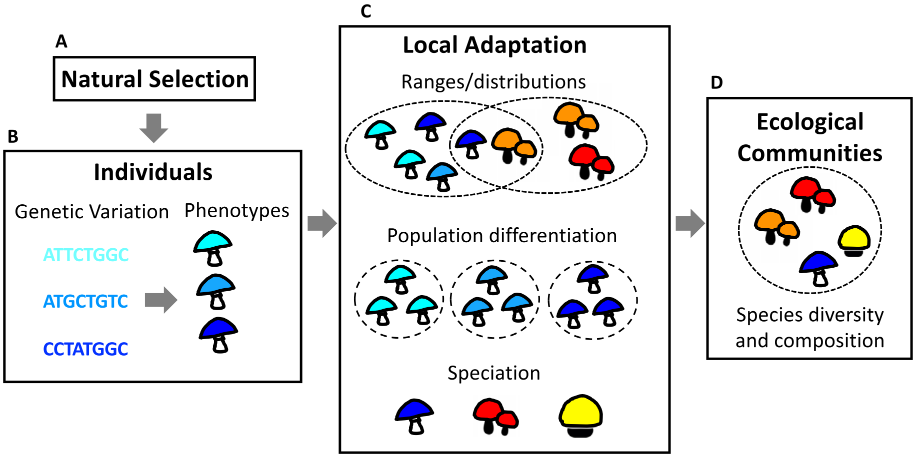

Fig. 1 – Adaptation shapes biological diversity. Natural selection (A) acts on phenotypes (B) and can lead to local adaptation, where individuals show higher fitness in their home environment (C). Local adaptation determines the limits of individuals' survival, impacting ranges and distributions, population differentiation and even lead to speciation. It also directly impacts ecological communities (D), by influencing species diversity and composition at local, regional, and continental scales.

Table 1 – Examples of documented adaptation in fungi with respective selective force and targets of adaptation.

Selective force	Fungus	Lifestyle	Target of adaptation	Reference
Chemistry	*Saccharomyces cerevisiae*	Saprobe	Copper transporter	Hull *et al.*, (2017)
	Suillus brevipes	Ectomycorrhizal	Membrane proton exchanger	Branco *et al.*, (2015)
	Suillus luteus	Ectomycorrhizal	Zinc transporters	Ruytinx *et al.* (2017)
				Coninx *et al.*, (2017)
Climate	*Neurospora crassa*	Saprobe	Helicase, pre-fold chaperone	Ellison *et al.*, (2011)
	Suillus brevipes	Ectomycorrhizal	Transmembrane transporters and helicases	Branco *et al.*, (2017)
Competition	*Metschnikowia reukafii*	Nectar yeast	Nitrogen scavenging	Dhami *et al.*, (2016)
Fungicides	*Candida* spp.	Human pathogen	Ergosterol synthesis	Whaley *et al.*, (2017)
	Cryptococcus neoformans	Human pathogen	Sterol synthesis	Kelly *et al.*, (1994)
				May *et al.*, (2015)
	Rhynchosporium commune	Plant pathogen	Calcium transporters, transcription activator, and saccharopine dehydrogenase	Mohd-Assad *et al.*, (2016)
	Zymoseptoria tritici	Plant pathogen	Ergosterol synthesis	McDonald *et al.* (2019)
				Estep *et al.*, (2015)
Host	*Entomophthora muscae*	Insect pathogen	Genes involved in utilization of host lipids and toxin secretion	Licht et al., (2016)
	Magnaporthe oryzae	Plant pathogen	Effector molecules	Liao *et al.*, (2016)
	Melampsora lini	Plant pathogen	Effector molecules	Barrett *et al.*, (2009)
	Microbotryum spp.	Plant pathogen	Effector molecules	Badouin *et al.*, (2017)
	Nectria haematococca	Plant pathogen	Pathogenicity	Miao *et al.*, (1991)
	Zymoseptoria tritici	Plant pathogen	Effector molecules	Poppe *et al.*, (2015)

contribute to determine which species inhabit particular sites. There has been increasing interest in trait-based approaches to understanding fungal communities (e.g. Peay *et al.*, 2011b, Branco *et al.*, 2013, Crowther *et al.*, 2014), however given the high diversity and cryptic nature of fungi, it has been difficult to identify key morphological/physiological traits affecting fungal fitness and determining species ranges and distributions. Furthermore, ecological studies assume such traits are static, even though it is known that adaptive traits not only evolve (Thompson, 1998) but can also influence priority effects (Urban and Meester, 2009, Knope *et al.*, 2012) and species coexistence (Lankau *et al.*, 2009, Vasseur *et al.*, 2011). Full understanding of fungal diversity and composition therefore requires both identifying relevant adaptive traits and documenting how they evolve and impact dispersal and establishment.

Few studies have addressed the evolution and genetic basis of adaptive traits in fungi and their impact in community assembly. The use of genomic approaches can provide invaluable information on how genetic diversity influences fungal community structure. Even though the use of whole genomes to understand community assembly is still in its infancy, it has been explored in nectar yeast communities. These simple systems, with low species richness and short generation times, are very amenable for both genomic and experimental approaches that have been used to investigate the phenotypic and genetic basis of species interactions and community assembly (Chappell and Fukami, 2018). In particular, whole genome studies in *Metschnikowia reukafii*, an ubiquitous nectar colonizing yeast displaying strong priority effects when competing with other species of nectar yeasts and bacteria (Vannette and Fukami, 2014), showed that genes involved in nitrogen scavenging (high capacity amino acid importers) are likely driving priority effects in nectar microbial systems (Dhami *et al.*, 2016). In addition, analyses of 102 *M. reukafii* whole genomes revealed no relationship between genetic variation and geographic distance but detected *M. reukafii* lineages correlated with metabolic ability and intraspecific competitiveness at both large and small spatial scales (Dhami *et al.*, 2018). Genomic studies addressing intraspecific genetic variation and the genetic basis of adaptation can therefore be linked to and complement fungal community assembly studies to significantly improve our understanding of overall fungal diversity.

3. Intra-specific variation is the foundation of evolutionary adaptation

Unveiling genotypic and phenotypic variation within species can make major contributions for identifying ecological niches and understanding biotic and abiotic interactions. However, so far little effort has been made to connect results from studies focusing on adaptation and species genotypic and phenotypic variation to investigations of community diversity and assemblage.

Adaptive evolution occurs as the result of natural selection acting on species/populations heritable variation (Charlesworth *et al.*, 2017) and directly impacts environmental requirements and limitations (Grant and Grant, 2011). This process occurs at the level of individuals and populations but determines species ranges and distributions (Fig. 1). Natural selection acts on phenotypes that result from genotypes and there has been an increasing interest in using genomic tools to determine the genetic basis of adaptation.

Evolutionary change as a response to environmental selection can have distinct genetic signatures, with adaptation targeting standing genetic variation, where alleles already present in the population at low frequency can confer increased fitness in novel environments and spread as a result of strong selection, or through novel mutations (Hermisson and Pennings, 2017). The genetic targets of selection vary according to the environment in question and can range from few to many genomic regions, with polygenic adaptation involving multiple loci under selection (Jain and Stephan, 2017). Furthermore, adaptation can arise through independent origins of adaptive alleles (Ralph and Coop, 2010), resulting from multiple mutations with similar phenotypic effects. Also, environmental adaptation can be rapid, with some studies documenting strong selection leading to evolutionary change over very short periods of time (Grant *et al.*, 2017, Campbell-Staton *et al.*, 2017, Donihue *et al.*, 2018, McDonald *et al.*, 2019). Many studies of adaptation investigate evolution under environmental stress and point to strong selective pressures acting on standing genetic variation, leading to the accumulation of genetic differentiation across individuals inhabiting distinct environments (e.g. Hendrick *et al.*, 2016, Reid *et al.*, 2016, Campbell-Staton *et al.*, 2017, Swarts *et al.*, 2017). Such studies compare individuals from distinct environments with the goal of detecting and characterizing the genomic regions under selection, as well as documenting the traits and phenotypes enabling adaptation. This last step of identifying adaptive candidate genes and testing their function allows for linking genotypes to phenotypes. Complementing this approach with experiments on genes with known phenotypic effects by measuring fitness in nature (Barrett and Hoekstra, 2011, Kraemer and Boynton, 2017, Barrett *et al.*, 2019) is crucial for a complete and accurate understanding of the evolution of adaptation.

The sources of genetic variation in fungi have been well documented (Taylor *et al.*, 2017) and include recombination and mutation, genome rearrangements (Branco *et al.*, 2018, Shi-Kunne *et al.*, 2018), gene gain/loss (Sharma *et al.*, 2014, Yoshida *et al.*, 2016) and gene family expansion and contraction (Baroncelli *et al.*, 2016, Gan *et al.*, 2016), changes in chromosome number (Miao *et al.*, 1991, Bertazzoni *et al.*, 2018), and horizontal gene transfer (Ropars *et al.*, 2015, Wang *et al.*, 2018). In addition, sexual reproduction is pervasive in fungi (Taylor *et al.*, 2015) and recombination long known to increase genetic variation and allow natural selection to be more efficient (Weissman, 1904, Barton and Charlesworth, 1998). Interestingly, the way sex facilitates adaptation to novel unhospitable environments was first demonstrated in yeast using experimental evolution. Genetic manipulation to create *S. cerevisiae* strains with different sexual reproduction capabilities and testing their performance under distinct environments showed sexual yeast lines had higher relative fitness under a harsh environment compared to asexual lineages (Goddard *et al.*, 2005). This said, fungal asexual lineages also undergo adaptation, with for example pathogenic clones adapting to novel environments in many cases of fungal invasions (Gladieux *et al.*, 2015, Robin *et al.*, 2017). Intraspecific variation is the foundation for adaptive evolution, so studies addressing fungal genetic variation are instrumental for understanding adaptation and diversity in fungi. However, the vast majority of studies addressing fungal genetic variation do not consider the ecological community context, missing species interactions as a precursor for establishment and fitness (Dhami *et al.*, 2018).

4. Natural selection drives adaptation and determines ecological niche

Natural selection acts on phenotypic variation and affects fungal ecology and species distributions, substantiating the value of addressing fungal diversity as a biological continuum, ranging from genes to ecological communities. Both abiotic and biotic factors can act as selective agents to structure fungal genetic diversity, with climate (Branco *et al.*, 2017, Feurtey *et al.*, 2016, Robin *et al.*, 2017), chemistry (Branco *et al.*, 2015, Estep, *et al.*, 2015, Hull *et al.*, 2017), and host (Miao *et al.*, 1991, Liao *et al.*, 2016, Licht, *et al.*, 2016) among the most well documented selective forces structuring fungal intraspecific diversity (Table 1).

Many studies on fungal environmental adaptation use targeted experimental approaches to investigate phenotypic differences across populations that can be quite effective at linking populations to environments (e.g. Adriaensen *et al.*, 2005, Torres-Cruz *et al.*, 2018). However, they require *a priori* knowledge of which environmental factors underlie adaptation that is often not available. Furthermore, such experiments might miss the bulk of adaptive genetic variation and do not necessarily provide a complete view of the genetic basis of environmental adaptation. Genomic studies of environmental adaptation on the other hand can provide improved insight into the patterns and mechanisms underlying environmental adaptation, even when the relevant selective forces are unknown (Li *et al.*, 2008, Taylor *et al.*, 2017). Combining genomic comparisons with no a priori local adaptation assumptions with functional tests validating candidate genes under selection offers an attractive and productive approach to investigating the ecology and evolution of fungi and better understand their niches and distributions, particularly in species for which little ecological information is available.

Both abiotic and biotic factors determine ecological niches and shape genetic diversity (Table 1). Climate is known for strongly influencing overall biological distributions (Garcia *et al.*, 2014, Isbell *et al.*, 2015, Zhou *et al.*, 2016), including in fungi with several examples of evolution of adaptation to specific climatic conditions explaining intraspecific variation and species range. Temperature in particular is known to affect fungal growth, survival, reproduction, and dispersal (Desprez-Loustau *et al.*, 2007) and fungal adaptation to local temperatures has been well documented, namely in the plant pathogens *Puccinia striiformis* (Mboup *et al.*, 2012), *Rhynchosporium commune* (Stefansson *et al.*, 2013), *Podosphaera plantaginis* (Laine, 2008), and *Zymoseptoria tritici* (Zhan and McDonald, 2011). *Cryphonectria parasitica*, the agent for chestnut blight originating from Asia and currently widespread across continents, is a good example on how the evolution of thermal adaptation allows for range expansion, leading to increased distribution areas. This species currently occurs in France, where the clonal populations from the south of the country that are adapted to high ambient temperatures evolved to tolerate colder environments and expanded north towards colder regions (Robin *et al.*, 2017). Temperature is also an important selective agent for non-pathogenic fungi. A population genomics study on *Suillus brevipes*, a widespread mycorrhizal North American fungus associated with pines, unveiled continental level population structure and local adaptation to both temperature and precipitation (Branco *et al.*, 2017). This study made no assumptions of what selective agents were acting on *S. brevipes* and by comparing whole genomes of individuals from seven localities across North America, the authors found population structure and high genetic differentiation at loci linked to transmembrane transport and helicase activity, known to play important roles in environmental sensing and cold and water stress. A similar and more comprehensive approach was taken by Ellison *et al.* (2011) to investigate local adaptation in *Neurospora crassa*. Whole genome comparisons of individuals across Louisiana and the Caribbean (differing on average by 9 °C in the winter months) identified differentiated loci in genes involved in temperature responses across populations, including a cold shock RNA helicase and a prefoldin chaperone known to protect actin from cold temperatures. The authors took advantage of the *N. crassa* gene deletion collection (Colot *et al.*, 2006) to perform functional tests that linked candidate genes to temperature tolerance. Further field reciprocal transplant experiments with mutants can confirm whether these genes are in fact responsible for the geographic distribution of the distinct locally adapted populations.

Chemical environments are also precursors of fungal adaptation. Heavy metals are well-known for leading to local adaptation in fungi, with tolerant ecotypes evolving to withstand toxic heavy metal levels. Examples of heavy metal tolerance have been documented in a wide range of fungi, including decomposers (Kaewdoung *et al.*, 2016, Torres-Cruz *et al.*, 2018), endophytes (Yamaji *et al.*, 2016), arbuscular mycorrhizal fungi (Meier *et al.*, 2015), ericoid mycorrhizal fungi (Daghino *et al.*, 2016), and ectomycorrhizal fungi (Reddy *et al.*, 2016). Fungal heavy metal tolerance often achieved through gene copy number variation, a known mechanism associated with fungal stress response (Wapinski *et al.*, 2007). A case study is *Suillus luteus*, a widespread Eurasian pioneer mycorrhizal fungus associated with pine trees and the dominant fungus in smelter regions in Belgium that have been enriched for Zn in the last ~150 y (Colpaert *et al.*, 2000, 2004, Op De Beeck *et al.*, 2015). This species occurs in nearby contaminated and non-contaminated soils and individuals from contaminated sites evolved adaptation to high Zn concentrations. Zinc adapted individuals are not only able to grow in much higher Zn concentrations, but also accumulate less Zn in their cells (Fig. 2). Molecular studies identified Zn transporter genes in *S. luteus* that affect Zn homeostasis, likely contributing for Zn tolerance. Specifically, *SlZnT1* and *SlZnT2*, two very similar genes that code for transporters in the cation diffusion facilitator family, were predicted to transport Zn out of the cytoplasm (Ruytinx *et al.* 2017). The high gene similarity suggests a recent gene duplication event. Functional analyses showed that *SlZnT1* played an important role in Zn accumulation and was constitutively expressed in *S. luteus*. The SlZnT1 protein transports excess Zn into the vacuole and is indispensable for the maintenance of Zn homeostasis. In addition, the membrane ZIP transporter SlZRT1 that is responsible for cell Zn uptake was also identified as relevant for Zn homeostasis in *S. luteus* (Coninx *et al.*, 2017). Heterologous expression in yeast confirmed the role and localization of this gene and gene expression assays revealed that *SlZRT1* expression is affected by external Zn concentrations. Gene copy number variation has also been reported as the mechanism underlying Cu tolerance in yeast (Hull *et al.*, 2017). Interestingly, in addition to the number of copies of the copper resistance gene *CUP1* being directly related to Cu adaptation in *S. cerevisiae*, there is also evidence showing high levels of environmental Cu induce copy number variation in *CUP1* (Hull *et al.*, 2017). Such environmentally stimulated copy number variation directly facilitates adaptation to novel environments, showing that fungi have the ability to implement genomic changes in response to environmental cues.

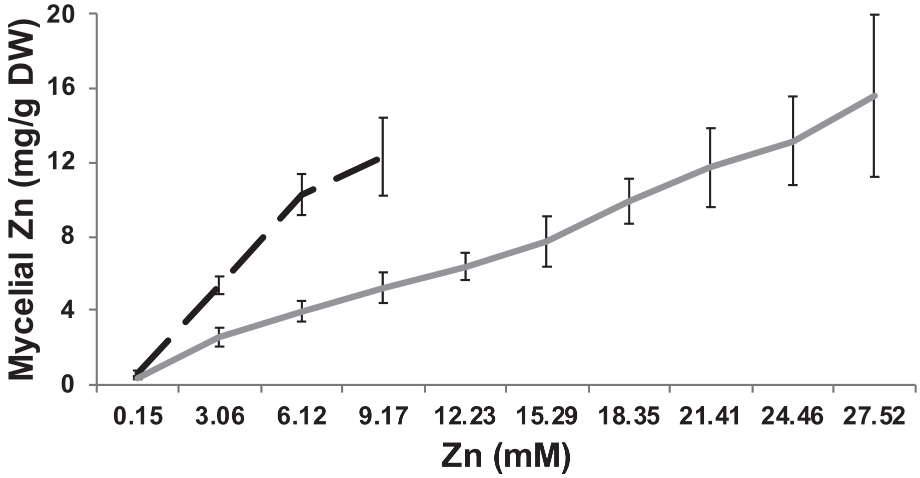

Fig. 2 – Zn tolerance in *S. luteus*. Differential tissue (mycelial) Zn content in isolates from Zn contaminated (gray) and non-contaminated sites (black) when exposed to a Zn gradient (adapted from Colpaert *et al*., 2011).

Antifungal resistance in fungal pathogens is another example of how fungi adapt to unhospitable abiotic conditions. For example, the use of pesticides in agricultural settings to improve crop yield is known to lead to rapid evolution of resistance that can have serious consequences, including threaten food security (Fisher, *et al*. 2018). *Zymoseptoria tritici* is a European wheat pathogen that causes septoria wheat blotch and is notorious for difficult control due to multiple antifungal resistance, including polygenic resistance to azoles (inhibitors of sterol biosynthesis) that are commonly used to control fungi (Leroux *et al*., 2007, Brunner *et al*., 2008, Cools and Fraaije, 2013). Antifungal resistance can evolve rapidly, as shown in studies documenting the evolution of tolerance to azoles and Quinone-outside Inhibitor fungicides (QoI; fungicides that disrupt cellular respiration) in *Z. triciti* over the span of 20 y in the United States (Estep *et al*., 2015), and over only 9 y in Australia (McDonald *et al*., 2019). Azole resistance is also well documented in *Rhynchosporium commune*, the agent for barley scald disease. This species evolved polygenic resistance differently from the known sterol biosynthesis-based resistance described in *Z. tritici*, including through mutations in genes coding for calcium transporters, a transcription activator, and saccharopine dehydrogenase (Mohd-Assad *et al*., 2016). Fungicide resistance is also well known in animal pathogens. Azole resistance in the human pathogens *Candida albicans* and *Cryptococcus neoformans* comes from specific mutations and increased expression of genes involved in sterol biosynthesis (Kelly *et al*., 1994, Whaley *et al*., 2017, May *et al*., 2016). The evolution of fungicide resistant isolates that have the ability to establish and persist despite control attempts leads to pathogen range and distribution extension, directly affecting local fungal assemblages and species interactions.

Biotic factors also shape fungal genetic diversity (Giraud *et al*., 2010). Fungi do not live in isolation and interactions with other species can have profound consequences for determining ecological niche, fitness and overall distribution. Biotic factors are particularly relevant in symbiotic species that live in close interactions with partners. Given the high impact of fungal pathogens on health and food security (Fisher *et al*., 2018), there is a wealth of literature regarding fungal host-pathogen interactions focused on understanding the evolution of fungal virulence, often with the ultimate goal of developing pathogen control and management strategies. The success of obligate fungal pathogens relies on the ability to evade ever evolving host defenses, leading to an evolutionary arms race where evolution in one partner induces evolution in the other partner (Dawkins and Krebs, 1979, Maor and Shirasu, 2005). This phenomenon shapes the genetic variation of both host and pathogen and often times leads to strict host specificity and the inability to infect multiple hosts (Ebert, 1998, Kawecki, 1998, Antonovics *et al*., 2013), restricting pathogen occurrence to where the suitable host is present and reducing competition with other pathogens (Licht *et al*., 2016). For example, the arms race between fungal plant pathogens and their hosts is well documented. Plant pathogenic fungi infect their hosts by secreting effectors that manipulate plant immune systems to allow successful infection, while plants respond by producing resistance proteins that trigger plant defenses and block fungal growth (Möller and Stukenbrock, 2017). Effector genes tend to undergo rapid evolution and can be located in accessory chromosomes, as first described in the pea plant pathogen *Nectria haematococca* (Miao *et al*., 1991). In this species, isolates having the accessory chromosome have a cluster of pea pathogenicity (PEP) genes that allows infection of pea plants, while isolates lacking the accessory chromosome infect other plants (Temporini and VanEtten, 2002). This implies that the PEP cluster is only involved in infecting pea plants and is not required for pathogenicity on other hosts, meaning that the presence of this accessory chromosome determines *N. haematococca* host range. Putative effector proteins have also been identified as key players in host species and genotype specialization for other plant pathogenic fungi, including the rust *Melampsora lini* (Barrett *et al*., 2009), *Zymoseptoria tritici* (Poppe *et al*., 2015), the rice blast fungus (*Magnaporthe oryzae*, Liao *et al*., 2016), and *Epichloë typhina* (Schirrmann *et al*., 2018).

Mutualistic associations (where partners benefit from each other's activities) also influence fitness. Many fungi form mutualisms with plants and can be highly specialized, associating with a restricted set of hosts (Gladieux, 2018). For example, endophytic fungi colonize living plant tissues without visible harm (Busby *et al.*, 2016) and are extremely rich and abundant in nature (Arnold and Lutzoni, 2007). There is ongoing debate on the prevalence of overall endophyte host specificity (Apigo and Oono, 2018), making it challenging to understand the drivers of endophytic community assembly and explain their observed high richness and diversity in nature. It is however clear that some fungal endophytes show clear host specificity (Wearn *et al.*, 2012).

Fungal plant mutualists can also influence the ecology of their partners by conferring stress tolerance and extending their habitat by allowing colonization of unsuitable habitats. Known examples include fungal endophytes enabling grass hosts to survive in geothermal and saline soils (Rodriguez *et al.*, 2008, Redman *et al.*, 2011), arbuscular mycorrhizal fungi improving plant growth in metal polluted soils (Meier *et al.*, 2015, Cornejo *et al.*, 2017) and ectomycorrhizal fungi conferring drought (Gehring *et al.*, 2017), heavy metal (Colpaert *et al.*, 2004, Adriaensen *et al.*, 2005, Hull *et al.*, 2017), and salt (Langenfeld-Heyser *et al.*, 2007, Li *et al.*, 2012) tolerance. Even though little data are currently available on the effects of adaptation on the ecology and evolution of their mutualistic partners, it is very likely that the evolution of stress tolerance in one mutualist shelters their partner from hostile environments, enabling persistence in sub-optimal or even lethal conditions in the absence of adaptation. Such mutualistic evolutionary sheltering (Fig. 3) contrasts with the arms race in pathogens in that adaptation in one species neutralizes natural selection and leads to evolutionary stasis in its partner. Given the ubiquity of mutualism in nature (including fungi and many other organisms) and the high rate of environmental shifts in face of climate change and anthropogenic activities, evolutionary sheltering is likely to be widespread in nature. It can significantly impact the ecology and evolution of mutualistic partners and should be further investigated for a comprehensive understanding of the effects of environmental shifts on biological diversity and the colonization of novel habitats.

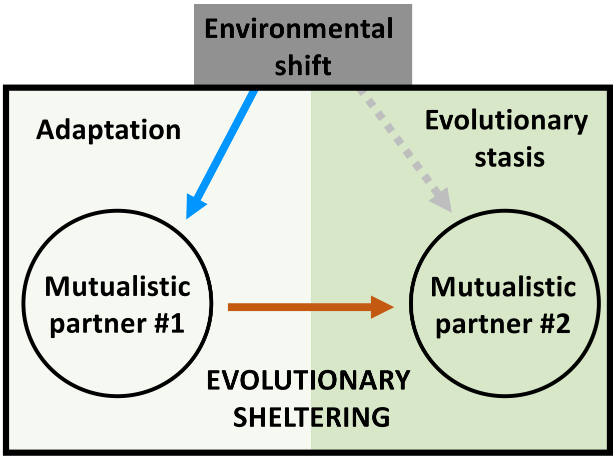

Fig. 3 – Evolutionary sheltering in mutualists. The process through which environmental shifts leads to the evolution of tolerance in a mutualistic partner (partner #1, left, blue arrow), which in turns shelters its partner from natural selection (partner #2, orange arrow), enabling persistence under the novel environment despite absence of adaptation (gray dashed arrow).

5. Conclusion

Full understanding of fungal diversity relies on studies encompassing distinct biological scales, from communities to species, populations, and genes. This implies combining rigorous documentation of fungal communities with in-depth knowledge of population-level diversity and the identification and understanding of key adaptive traits influencing fungal dispersal and establishment. Such approach will not only allow to make direct links between diversity, environments and adaptation, informing on how current fungal diversity originated and is maintained, but also develop models to make predictions on the future of fungal diversity.

Future research efforts should focus on addressing pertinent emerging questions in the field, including 1) how does genetic diversity influence community assembly?, 2) does intraspecific genetic variation affect fungal functional roles?, 3) what are the key adaptive traits in fungi?, and 4) how does adaptation affect symbioses? Answering these questions will most likely be made easier in the near future when advances in sequencing technology and analyzes allow for assembling high quality fungal genomes directly from environmental samples, enabling simultaneous studies of communities and populations. Having access to fungal cultures and the ability to conduct experiments testing for adaptation will however remain a challenge. Simple fungal systems with low species diversity that are amenable for experimental approaches, such as nectar yeasts (Chappell and Fukami, 2018), are very suitable for combining above- and below-species level studies and can provide significant contributions for a better and comprehensive understanding of fungal diversity and adaptation. Complex and highly diverse communities will continue to be more difficult to address. However, it is still possible to coordinate information on the ecology and evolution of specific clades to better understand their diversity. These model clades are lineages for which there is phylogenetic, genetic, and functional knowledge and that enable the understanding of specific concepts, such as community assembly and environmental adaptation (Cavender-Bares, 2019). The ectomycorrhizal genus *Suillus* is a good example of a fungal model clade, as there have been concerted efforts to generate and integrate knowledge in systematics, ecology, and genomics (http://www2.hawaii.edu/~nn33/suillus/) that are enabling a much better understanding of the ecology and evolution of the genus that can also inform other mycorrhizal fungi. Combining information at a multitude of biological levels for other fungal clades and systems will yield direct links between genetic variation, adaptation, and environments and provide a much more comprehensive understanding of fungal diversity.

Conflict of interest

The author has no conflict of interest to declare.

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Glossary

Community ecology
Study of a set of species co-occurring and interacting in space and time

Population genetics
Study of genetic variation and evolution within populations over space and time

Demography
Statistical study of populations, including their size, structure, and distribution

Genetic variation
Pool of alleles present in a group of organisms

Natural selection
Differential survival and reproduction due to phenotypic differences

Adaptation
Change in traits as a response to selection

Ecological niche
Role and position of a species within an ecosystem

Local adaptation
The evolution of traits providing advantage in local conditions

Ecotype
Locally adapted population

Speciation
Process by which populations evolve to become new species

Dispersal limitation
The inability of organisms to colonize all sites

Priority effects
When the arrival order and initial abundance of species determines community composition

Competition-colonization trade-offs
The compromise between the ability to colonize a site and the ability to competitively displace established species

Standing genetic variation
Existing genetic variation in a population

Polygenic adaptation
Adaptive change due to shifts in allele frequencies of many loci

Mutation
Change in the nucleotide sequence of a genome

Recombination
Exchange of genetic material

Genome rearrangement
Large alteration of chromosomes or chromosomal regions

Horizontal gene transfer
Movement of genetic material between organisms by mechanisms other than vertical inheritance

Candidate genes
Genes putatively underlying traits of interest

Copy number variation
When the number of copies of a particular gene varies across individuals

Accessory chromosomes
Non-essential chromosome additional to the regular karyotype of a species

Evolutionary sheltering
When a mutualist adapts to an environmental shift and shields its partner from selection, allowing it to persist without adapting

Model clades
Biological lineages that enable advancements in the understanding of specific concepts

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fbr.2019.06.003.

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