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Fungal functional ecology: bringing a trait-based approach to plant-associated fungi

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ABSTRACT

Fungi play many essential roles in ecosystems. They facilitate plant access to nutrients and water, serve as decay agents that cycle carbon and nutrients through the soil, water and atmosphere, and are major regulators of macro-organismal populations. Although technological advances are improving the detection and identification of fungi, there still exist key gaps in our ecological knowledge of this kingdom, especially related to function**.** Trait-based approaches have been instrumental in strengthening our understanding of plant functional ecology and, as such, provide excellent models for deepening our understanding of fungal functional ecology in ways that complement insights gained from traditional and -omics-based techniques. In this review, we synthesize current knowledge of fungal functional ecology, taxonomy and systematics and introduce a novel database of fungal functional traits (Fun^{Fun}). Fun^{Fun} is built to interface with other

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databases to explore and predict how fungal functional diversity varies by taxonomy, guild, and other evolutionary or ecological grouping variables. To highlight how a quantitative trait-based approach can provide new insights, we describe multiple targeted examples and end by suggesting next steps in the rapidly growing field of fungal functional ecology.

Key words: clades, ecology, endophytes, evolution, functional traits, fungi, guilds, mycorrhizae, pathogens, saprotrophs, taxonomy.

CONTENTS

I. INTRODUCTION

In ecosystem functioning, diversity, and human use, fungi are dominant but often hidden components of terrestrial ecosystems (Gadd, 2006; Stajich *et al.*, 2009; Blackwell, 2011; Kendrick, 2011; Hawksworth & Lücking, 2017; Steidinger *et al.*, 2019). They are perhaps best known as dead organic matter decomposers, which makes them essential for cycling of carbon and other nutrients through Earth's ecosystems and atmosphere (Rayner & Boddy, 1988; Floudas *et al.*, 2012; van der Wal *et al.*, 2013). Fungal biochemical pathways have been harnessed for myriad processes, including production of food, medicine, biofuels and other commodities. Conversely, fungal pathogens cause major losses in global food production (Strange & Scott, 2005; Schmaile & Munkvold, 2009; Fisher *et al.*, 2012). Fungi have had a long and intimate association with plants. As root- and leaf-associated symbionts, fungi directly affect richness and productivity of present-day plant communities (van der Heijden *et al.*, 1998; Bakker *et al.*, 2012; Mueller, Belnap, & Kuske, 2015), and these symbioses may have been key to colonization of land by plants (Chisholm *et al.*, 2006; Krings *et al.*, 2007; Johnston-Monje & Raizada, 2011; Lutzoni *et al.*, 2018).

Recent estimates suggest that the number of extant fungal species on Earth may be between 2–4 million (Hawksworth & Lücking, 2017) and 165.6 million (Larsen *et al.*, 2017), significantly outnumbering known plant species, which are estimated at ∼350,000–400,000 species (Mora *et al.*, 2011; Larsen *et al.*, 2017; https://stateoftheworldsplants.org/; http://www.theplantlist.org/). Most species, however, are too small or cryptic to be detected with the naked eye. We have long distinguished various fungi from fruiting bodies or cultures, but most fungi do not fruit regularly or grow in culture. The advent of high-throughput sequencing (HTS) provided an important lens through which to view the taxonomic and functional diversity of these eukaryotes that would otherwise remain undetected or unidentified (Peay, Kennedy, & Talbot, 2016). Using HTS and other molecular tools, we can now ascertain patterns of fungal diversity and community assembly across space and time, as well as detect functional

genes and gene products of particular groups that may drive community assembly processes (Tedersoo *et al.*, 2014).

Given the dominant role fungi play in the function of different systems (Gadd, 2006; Stajich *et al.*, 2009; Blackwell, 2011; Kendrick, 2011; Hawksworth & Lücking, 2017; Steidinger *et al.*, 2019), there is an urgent need to improve our understanding of the functional and ecological diversity of fungi. Here, we highlight recent advances and key gaps in our knowledge of functional ecology in the kingdom fungi. We also provide an overview of the state of fungal systematics and taxonomy, as adopting uniform clade names across disciplines is critical for linking across databases and placing taxa in an evolutionary framework. Trait-based approaches have provided important insights for other taxa, such as plants (Kattge *et al.*, 2011; Maitner *et al.*, 2018). Indeed, fungal association type is an explicit trait linked to many plant taxa and used to infer plant nutrient-uptake strategies [but see Brundrett & Tedersoo, 2019 for a discussion of concerns regarding data quality]. We discuss a similar approach for gaining a deeper understanding of fungal ecology and evolution. Additionally, we make significant progress towards filling these gaps by presenting a novel, open and dynamic database of fungal functional traits (Fun^{Fun}). Fun^{Fun} can directly interact with the curated, open-source fungal ecological guild database (FUNGuild; Nguyen *et al.*, 2016), allowing researchers to explore critical dimensions of fungal functional diversity and map taxonomic, genomic, and functional data within and across fungal guilds. Although our database is not limited to specific fungal groups, in this review, we focus on plant-associated fungi – predominantly endophytes, pathogens, mycorrhizal fungi, and saprotroph guilds – as this will allow a broad suite of questions, e.g. exploration of the coordinated ecological function of fungi and their associated plant clades through a trait-based approach due to the large body of work in existence in plant functional ecology. We address three fundamental questions about plant-associated fungi: what is currently (1) known and (2) unknown about these fungal groups, and (3) how can we use a trait-based approach to advance our knowledge? Additionally, we present two targeted studies illustrating specific ways that a quantitative trait-based approach can be broadened to add insight into fungal function and end with recommendations towards future progress for fungal functional ecology. Combined, our review and new data resource lay the framework for rapid progress on fungal functional ecology in the future.

II. TRAIT-BASED PERSPECTIVES ON FUNCTIONAL ECOLOGY

(1) Developing a fungal functional trait-based approach: lessons from plant ecology

'Traits' include a wide range of organismal characteristics. In plants, where a trait-based approach has a rich history extending back at least to 300 years BC (Theophrastus, 1916; Blackman, 1920; Bloom, Chapin, & Mooney, 1985), some of the most useful have been continuous phenotypic characteristics, such as seed size, maximum plant height, and specific leaf area, relevant to their carbon, nutrient, and water economies (see Table 1, which includes comparable traits to measure in fungi; Pérez-Harguindeguy *et al.*, 2013; Reich, 2014). Such traits underpin an organism's ecological strategy (MacArthur & Wilson, 1967; Grime, 1974) and can directly impact its fitness, tolerance to abiotic conditions, resource use, and/or competitive ability. Trait values have been especially useful in placing a measured individual into an informative context, including the distribution of extant trait values in its clade (Cornwell *et al.*, 2014) or distribution of locally co-occurring trait values in a given environment (Wright, Reich, & Westoby, 2001).

Trait values are a product of evolution shaped by ecology; that is, mutation, drift, and selection operating under each individual's interactions with its environment and other organisms. One of the key tenets of functional trait ecology is that portions of trait space may lead to common trait combinations even across phylogenetically distant groups, but others may be strategically unsuccessful (either locally or globally) for one of two reasons: (1) fundamental biochemical, biophysical, or genomic limitations prevent individuals from moving into parts of trait space, and/or (2) species within parts of trait space are poor competitors relative to successful taxa (Reich, Walters, & Ellsworth, 1997). Traits thus include tradeoffs and adaptive elements that may be understood better as constraints between different functions with conflicting costs and benefits (Bloom *et al.*, 1985; Westoby *et al.*, 2002; Reich *et al.*, 2003). Many of these constraints have yet to be formally examined across fungal species (Zanne *et al.*, 2019), but will likely structure how communities assemble and shape emergent ecosystem functions of these communities, including rates of organic matter decomposition and nutrient release (Fernandez & Kennedy, 2018).

(2) Utility of a trait-based perspective for fungal functional ecology

Fungal species have long been sorted into ecological strategies or guilds, although strict assignment of a given species to a particular guild is currently receiving scrutiny (e.g. various fungal species can move among guilds; see Fig. 1 and Section IV). For plant-associated fungi, we focus on the following guilds: endophytes (Link, 1809; Hardoim *et al.*, 2015), pathogens (Bassi, 1835), saprotrophs or saprobes (Martin, 1932; Ainsworth, 2009), and mycorrhizal fungi (Frank, 1885; Rayner, 1926). A guild is defined by the resource use of its members. Endophytes inhabit living plants and do not cause disease (Petrini, 1991), whereas fungal pathogens cause disease when obtaining nutrients from their host (Mendes *et al.*, 2011; Casadevall & Pirofski, 2014; Hyde *et al.*, 2014). Saprotrophic fungi obtain energy and nutrients by breaking down dead organic plant material (reviewed in Dighton, 2016), and mycorrhizal fungi facilitate plant nutrient uptake in exchange for photosynthetic carbon from their host plants (Smith & Read, 2008). These strategies

Table 1. Important plant traits, their economic/functional strategy, potentially comparable fungal traits, and hypotheses for their role in fungal strategies

Economy/function	Plant trait	Comparable fungal trait	Hypothesised role in fungi
Reproductive allocation	Seed size/seed number (Moles & Westoby, 2006)	Spore size/spore number (Aguilar-Trigueros *et al.*, 2019)	A tradeoff between spore size and spore number exists. The numerical advantage of large spore number will be counteracted by higher survival of larger spores. There will be no difference in total allocation to reproduction over an individual's lifetime.
Reproduction	Maximum height (Thomson *et al.*, 2011)	Maximum fruiting body size (Dressaire *et al.*, 2016)	Species with larger fruiting bodies will bear larger spores. Bigger fruiting bodies will disperse spores further.
Water, nutrient uptake	Specific root length (McCormack *et al.*, 2015)	Specific hyphal length (Lovelock, Wright, & Nichols, 2004)	Higher specific hyphal length will be related to faster strategies – higher hyphal nutrient content, shorter lifespan, and faster growth rates. Higher specific hyphal length will allow more rapid water and nutrient uptake.
Carbon allocation	Lignin content (Melillo, Aber, & Muratore, 1982; Poorter *et al.*, 2004)	Melanin content (Fernandez *et al.*, 2019)	Species with higher melanin content will be less susceptible to fungivory and decomposition. They will also sustain slower growth rates and have longer-lasting tissue lifespans.
Nutrient allocation	C:N:P (Reich & Oleksyn, 2004)	C:N:P (Zhang & Elser, 2017)	Species with higher ratios of N and/or P to C will sustain higher growth rates and have faster returns on tissue nutrient investment.
Size-related scaling	Plant body size (Niklas, 1994)	Fungal body size (Aguilar-Trigueros, Rillig, & Crowther, 2017)	While difficult to measure, larger fungi will have denser tissues, slower growth rates and longer lifespans. Metabolic rates will scale with body size.
Carbon, nutrient uptake	Extracellular compounds, such as carnivorous digestive enzymes (Mithöfer, 2017) and root exudates (Lynch & Brown, 2008)	Extracellular enzymes (Joner & Johansen, 2000; Snajdr *et al.*, 2011)	Fungi growing in nutrient-poor systems will invest in extracellular enzymes to extract those resources.

represent the current state of our understanding of functional ecology across plant-associated fungi, but a trait-based perspective could move us forward by identifying key trait combinations that characterize each guild (Chagnon *et al.*, 2013; Aguilar-Trigueros *et al.*, 2014; Crowther *et al.*, 2014; Treseder & Lennon, 2015). For instance, fungal pathogens are characterized by increased genetic capacity for secreted effector proteins compared to saprotrophs, some of which confer virulence (Ohm *et al.*, 2012; Peay *et al.*, 2016). Similarly, mycorrhizal fungi generally produce fewer extracellular enzymes targeting complex organic compounds than do saprotrophs (Riley *et al.*, 2014; Kohler *et al.*, 2015; Talbot *et al.*, 2015). To date, patterns such as these have typically been characterized using just a few species and a subset of functional guilds for any given study. By comprehensively examining the variation of specific traits among and within guilds, we can reassess our concept of guild boundaries and identify complex mechanisms associated with these guilds better, including trait and guild effects on other organisms and across ecosystems.

The analysis of trait relationships among fungi can also highlight potential evolutionary or physiological tradeoffs that shape responses of functional guilds to environmental pressures (Treseder, Kivlin, & Hawkes, 2011; Wallenstein & Hall, 2012; Crowther *et al.*, 2014; Martiny *et al.*, 2015; Halbwachs, Heilmann-Clausen, & Bässler, 2017). Recent papers focus on traits critical to how fungi make their living, including body/thallus size, growth rate, respiration rate, spore size, stress tolerance (especially *via* melanin production), demand for nitrogen (N) and phosphorus (P), extracellular enzyme production, and development of hyphae *versus* budding growth (Wallenstein & Hall, 2012; Chagnon *et al.*, 2013; Aguilar-Trigueros *et al.*, 2014; Crowther *et al.*, 2014; Koide, Fernandez, & Malcolm, 2014; Eichlerová *et al.*, 2015; Treseder & Lennon, 2015; Peay *et al.*, 2016; Nagy *et al.*, 2017; Siletti, Zeiner, & Bhatnagar, 2017; Zhang & Elser, 2017; Calhim *et al.*, 2018), They also demonstrate correlations between traits and climate or substrate preference (Kauserud *et al.*, 2011; Nordén *et al.*, 2013; Heilmann-Clausen *et al.*, 2014; Andrew *et al.*, 2016; Abrego, Norberg, & Ovaskainen, 2017;

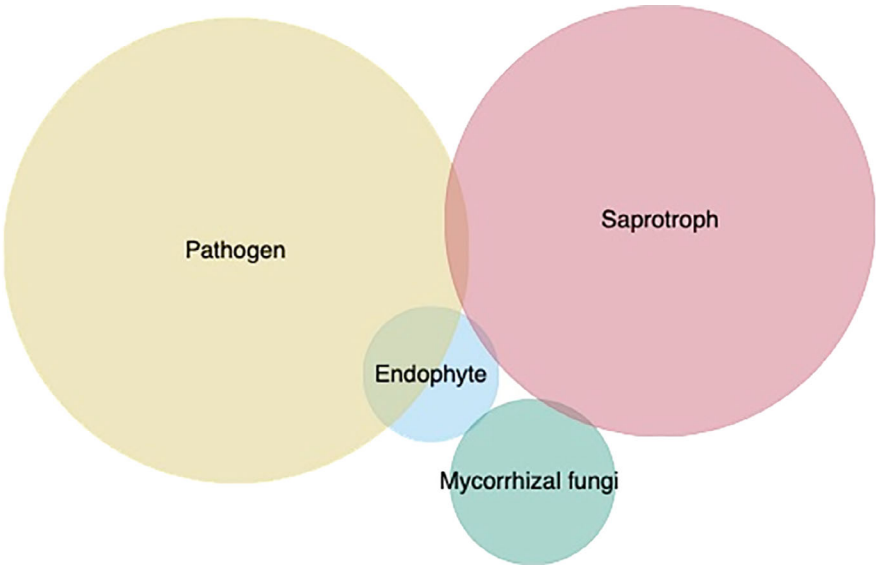

Fig. 1. The diversity and overlap of taxa in ecological guilds from FUNGuild (Nguyen *et al.*, 2016). The total number of taxa included is 7678. Circle size denotes the number of taxa in that guild with pathogens (tan), mycorrhizal fungi (green), endophytes (blue), and saprotrophs (pink).

Halbwachs *et al.*, 2017; Krah *et al.*, 2018), especially those traits that underpin species' abilities to disperse, colonize, and establish in different environments. For instance, spore size, wall thickness, and ornamentation differ among guilds and clades, and in some cases determine where particular individuals establish (Kauserud *et al.*, 2011; Nordén *et al.*, 2013; Halbwachs, Brandl, & Bässler, 2015; Andrew *et al.*, 2016; Abrego *et al.*, 2017; Halbwachs *et al.*, 2017; Calhim *et al.*, 2018). As we identify axes of trait variation, we can further determine how boundaries of trait combinations are shaped by competitive advantages and biochemical, biophysical, or genomic limitations (Reich *et al.*, 1999), in particular by environmental settings and among different ecological guilds and evolutionary clades.

(3) What can we learn from fungi? Unique contributions of fungal functional approaches

(a) *Small spaces, short times, big results*

A frequently cited reason for using microbial systems to test outstanding hypotheses in ecology and evolution is the power to manipulate populations and communities, with high replication at spatially and temporally tenable scales. Many of these attempts have focused on bacteria, but fungi offer a number of advantages. Fungi span a range of scales, from short-term (seconds to minutes) micron-level dynamics to emergent observable patterns that can reach hectares and represent months or years (Ferguson *et al.*, 2003; Peay, Kennedy, & Bruns, 2008). Additionally, because of the short time frame and small spatial scale under which fungal experiments can be conducted, they provide valuable opportunities for testing hypotheses that are infeasible in larger-bodied groups (Maherali & Klironomos, 2007; Maynard *et al.*, 2017). Furthermore, fungi can be used to test ecological theories developed in macro-scale systems to see if they hold at smaller scales where ecological theory has not previously been developed (Prosser *et al.*, 2007; Christian, Whitaker, & Clay, 2015).

It is important to note that in fungi, trait effects are often measured in controlled conditions (e.g. petri plates, growth chambers, greenhouses) on known isolates. The ability to run experiments in small spaces over short time scales with fungi allows for HTS for multiple traits of ecological importance. Because trait effects may be different in natural *versus* controlled conditions, extrapolation of results from the laboratory to the field should be done with caution. However, examples exist in which laboratory experiments provide important insights into the effect of traits on fungal function in natural settings, including mycoparatism and pathogenicity (Halleen, Mostert, & Crous, 2007; Van Wyk *et al.*, 2010). For instance, mycoparasitism-associated traits, such as directed growth toward target fungi, attachment and coiling on target fungi, and production of antifungal extracellular enzymes, can be observed in dual-culture plate assays (Benítez *et al.*, 2004; Harman *et al.*, 2004). The presence of these traits predicted the outcome of a three-partite interaction among a host, a pathogen, and an endophyte mutualist. Various *Trichoderma* species and strains isolated as endophytes and characterized as having mycotrophic traits *in vitro* (dual assays) were later inoculated into host plants, successfully reducing the presence of a fungal plant pathogen and consequently reducing and/or preventing disease in the host (Pujade-Renaud *et al.* (2019); Lahlali & Hijri, 2010; Park *et al.*, 2019). As fungal traits are measured in the laboratory and tested in the field, their utility can be increased by documenting experimental conditions and cataloguing fungal strains for future.

(*b*) *It's all in the partnership: understanding function by integrating plant and fungal traits*

We are continually learning about co-dependent plant–fungal associations that are profoundly interwoven with the plant traits we use to predict plant fitness and ecosystem function (Friesen *et al.*, 2011; Jacobs *et al.*, 2018; Pither *et al.*, 2018); utility of the trait-based approach for predicting such outcomes is likely to improve as we integrate fungal and plant traits into our analyses (Van der Wal *et al.*, 2016; Zobel, 2018). Mycorrhizal fungi are a prime example of a mutualism where fitness of the plant extends beyond traits of the plant root to traits of the mycorrhizal fungi. A flexible association with colonizing fungi suggests that a diversity of fungal traits might influence plant nutrition in the absence of a difference in plant traits. Similarly, wood-degrading fungi have flexible 'host' associations, and their nutritional modes (rot strategies) are not redundant (e.g. lignin-degrading 'white rot' *versus* carbohydrate-selective 'brown rot'). Traits of wood-degrading fungi colonizing a given log can drive different fates for carbon (Song *et al.*, 2012). Furthermore, plant traits and climate can be poor predictors of wood decomposition rates, and traits of these fungi that dominate the decay process likely explain a large fraction of the observed variability (Bradford *et al.*, 2014; Cline *et al.*, 2017; Song *et al.*, 2017; Steidinger *et al.*, 2019).

(*c*) *Broad-spectrum toolboxes*

The 'toolboxes' developed for fungi have largely been forged in a different context from those developed for plant and animal systems. For example, due to their numerous applications in industry, various fungi already have well-described genomes. Genetic engineering and post-genomic modifications have also been performed using fungi, with the intent to optimize production of industrial enzymes (Himmel *et al.*, 2007) and secondary metabolites (e.g. statins; Endo, 2010). Immense -omics toolkits have been developed for many of these fungi, and the target number of sequenced and annotated genomes continues to increase (Grigoriev *et al.*, 2014). Such resources can link fungal structure and function at scales from individuals to communities. For example, loss of wall-degrading enzymes in ectomycorrhizal fungi that were present in their ancestral wood-decaying fungi was detected using newly sequenced fungal genomes (Kohler *et al.*, 2015). Similarly, availability of a high-quality mycorrhizal genome allowed for detection of genes in the fungi that are co-expressed with host genes, providing insight into complementary functions and traits across the fungi–plant symbiotic boundary and how they change in response to the presence of rhizobia (Palakurty, Stinchcombe, & Afkhami, 2018). Furthermore, targeted genetic approaches, such as knockouts, can be utilized to develop links between genes and traits. For example, manipulation of ergot alkaloid profiles of plants through the knockouts of two endophyte genes allowed researchers to differentiate between ergot alkaloid effects and other endophyte-associated effects on plant hosts and rodent herbivores (Panaccione *et al.*, 2006). Generally, selection of which genomes to sequence has been based on 'useful' taxa for applied problems but more recently taxa have been selected across guilds and clades (e.g. 1000 Fungal Genomes Project; Grigoriev *et al.*, 2011, 2014). These samples are non-random, but such focus also drives the development of tools and resources that can be translated to other taxa and well beyond their primary intended purposes.

(4) The Fun^{Fun} database for fungal functional traits

To explore diversity in trait space across all fungi and compare these empirical findings to existing knowledge from different parts of the fungal tree of life from reviewing the literature, we introduce a novel Fungal Functional Trait Database (Fun^{Fun}) collated from published and novel data sets across the fungal tree of life (Fig. 2; for further information see https://github.com/traitecoevo/fungaltraits). Fun^{Fun} is designed as a living data set for which taxonomy and guild definitions update as they change and new information is easily incorporated, as measurements and compilations of trait data currently lag behind other databases for fungi (Fig. 3). Updates on this data set correspond to new versions, allowing users to access current and past versions, increasing reproducibility. After constructing architecture of the living dynamic database, we filled it with exemplar studies with accessible data. At this initial phase, information stored in the database is fairly limited. We consider our initial analyses presented here preliminary; however, as the community adds information, the number of species, traits, and measures will expand (to submit data see readme at https://github.com/traitecoevo/fungaltraits). To date, we include around 80 traits (for further information see https://github.com/traitecoevo/fungaltraits) encompassing genetic, enzymatic, morphological, stoichiometric, life history, and physiological aspects of fungi to highlight the state of empirical fungal functional ecology. The current 1.0.0 version of this database uses the Index Fungorum (http://www.indexfungorum.org) taxonomic nomenclature and contains 25,864 measurements, for 3104 species distributed across 1611 genera, 267 families, and 107 orders.

In joining the Fun^{Fun} functional trait database to FUNGuild (Nguyen *et al.*, 2016) in our analysis, we find that trait information exists across all plant-associated guilds and major clades; however, this information is not evenly distributed across guilds and clades (Figs 4 and 5). For instance, trait data are available for 7% of the 8207 Ascomycota genera, 18% of the 2161 Basidiomycota genera, 20% of the 196 Zygomycota genera, and 15% of the 208 genera in other clades. Additionally, for genera present in our database, guild is only known for 11% of the accepted Ascomycota genera and 8% of the accepted Basidiomycota genera (Nguyen *et al.*, 2016). Similarly, we know less about endophytes and pathogens than other guilds (Figs 4 and 5A). Finally, our trait list is large but still growing. We know least about physiological traits across the tree of fungal life (Figs 2 and 5). We should note that in both our literature (see Section V) and database queries (Fig. 1), we find that a given species of

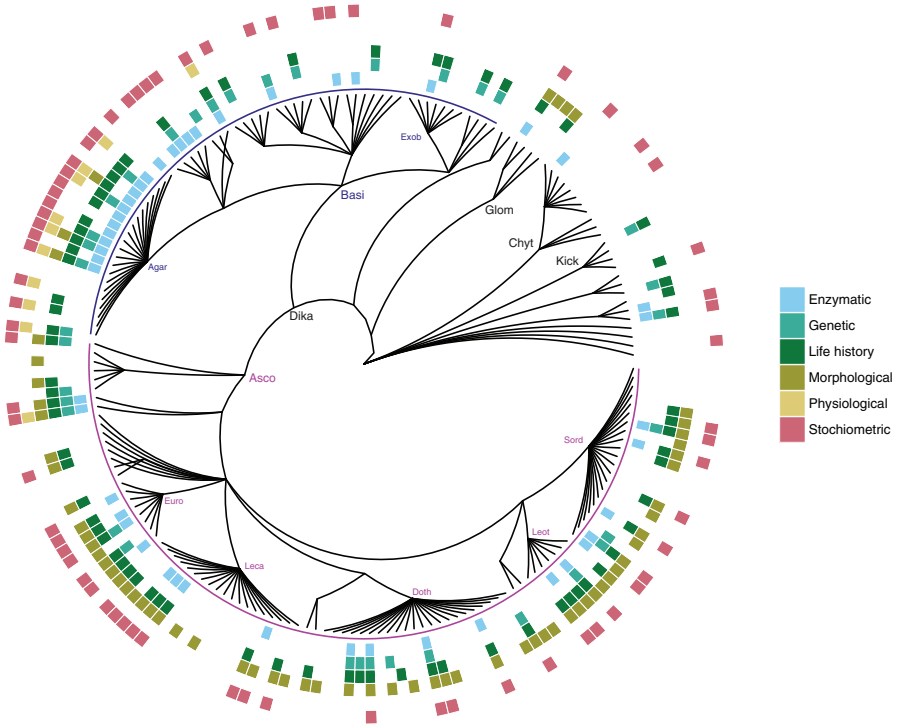

Fig. 2. Trait distribution [presence/absence in the Fungal Functional Trait Database (Fun^{Fun})] across the fungal phylogeny for 2190 species. Tree topology was constructed manually following Hinchliff *et al.* (2015) and Open Tree of Life (https://tree.opentreeoflife.org/opentree/opentree10.4@ott352914/Fungi). The phylogeny is order level and branch lengths are not time calibrated. Agar, Agaricomycetes; Asco, Ascomycota; Basi, Basidiomycota; Chyt, Chytridiomycota; Dika, Dikarya; Doth, Dothideomycetes; Euro, Eurotiomycetes; Exob, Exobasidiomycetes; Glom, Glomeromycota; Kick, Kickxellomycotina; Leca, Lecanoromycetes; Leot, Leotiomycetes; Sord, Sordariomycetes. Taxa in Ascomycota are denoted in purple, Basidiomycota in blue and other clades in black. Traits were pooled into five major trait categories: enzymatic (light blue), genetic (aqua), life history (green), morphological (brown), physiological (tan), and stoichiometric (pink). The traits in each category are listed in the fun_processing.R file in Fun^{Fun} (https://github.com/traitecoevo/fungaltraits).

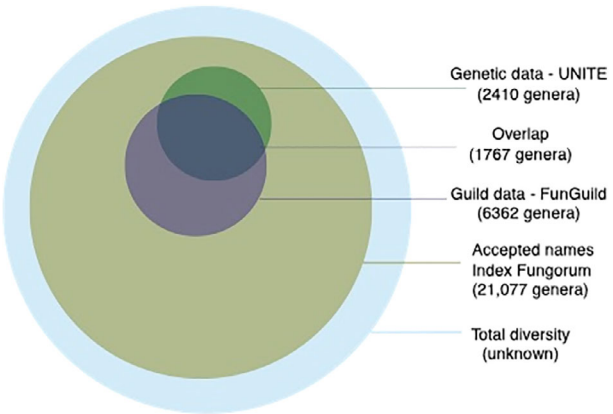

Fig. 3. Generic overlap among data sources for fungi. When comparing the number of genera that overlap among the major data sources for this project, total diversity (light blue) is unknown; however, of accepted fungal genera found in Index Fungorum (http://www.indexfungorum.org; light green), genetic data from UNITE (https://unite.ut.ee/; dark green), and guild data from FUNGuild (Nguyen *et al.*, 2016; purple) form a small subset, with overlap among all three databases (black) smaller still.

fungi may be classified to more than one guild, but the degree to which individuals or species of fungi move among guilds is still poorly recorded (see Section IV). Information gaps such as these highlight the need for community involvement in expanding and refining these databases.

For the five traits for which we have most records (fruiting body size, melanin content and stoichiometric ratios – N:P, C:N and C:P), we partitioned trait variation at different taxonomic levels from above family to intraspecific, the latter included in 'unexplained' (Fig. 6A). Unexplained variation, including intraspecific, was modest (27–51%). Most explained variation was partitioned at genus and higher taxonomic levels, with the exception of N:P for which 'species' variation (43%) was higher than variation at higher taxonomic levels (25%). For these same traits, if we compare distributions among pathogen, saprotroph and mycorrhizal guilds, they show tantalizing differences for fairly small data coverage with fruiting body sizes, C:P, and N:P larger in mycorrhizal fungi and fruiting body size and melanin content smaller in pathogens [Fig. 6B; see also Zhang & Elser, 2017 regarding C:N:P patterns associated with fungal guilds]. It will be interesting to see whether these patterns remain robust as additional species are added to the database.

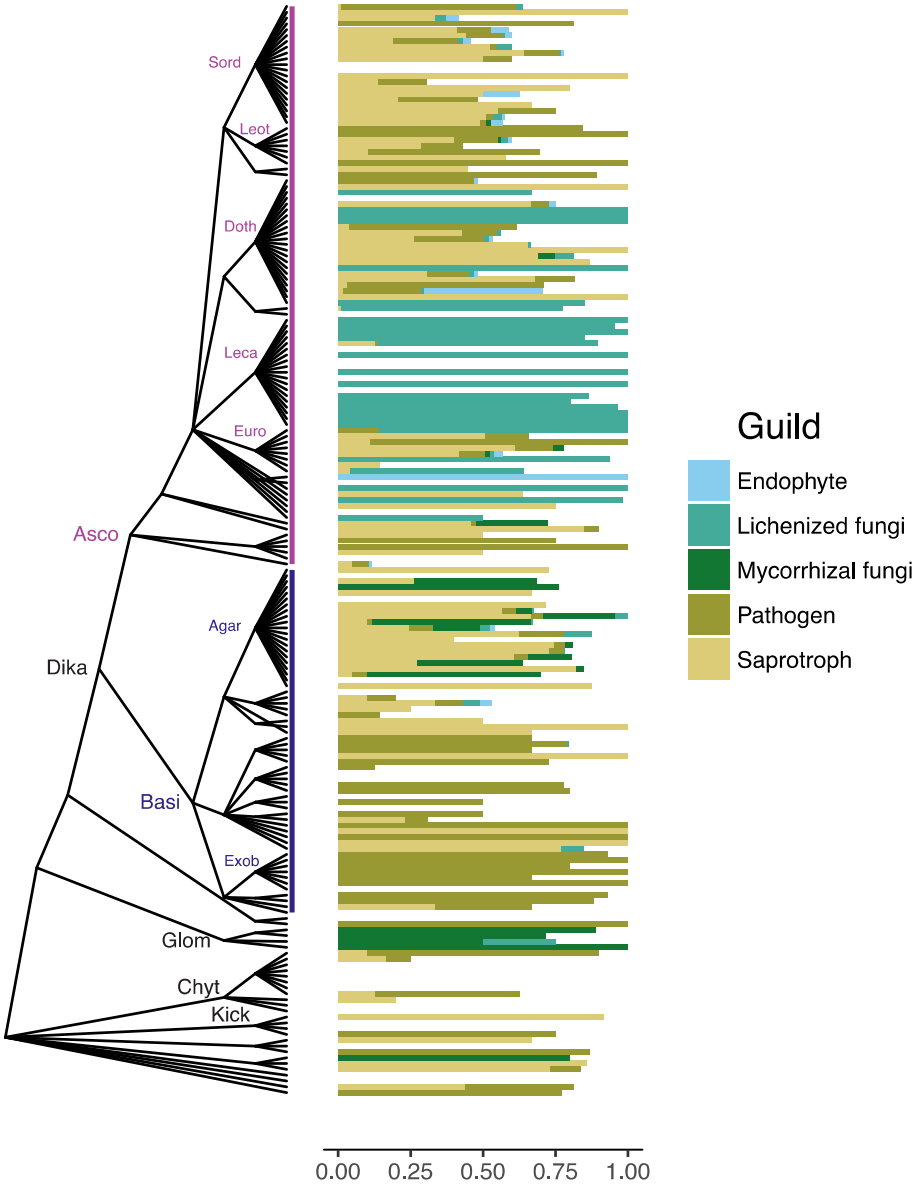

Fig. 4. Proportion of genera out of the total present in an order that belong to a given plant-associated fungal guild (endophytes in light blue, lichenized fungi in aqua, mycorrhizal fungi in green, pathogens in brown, and saprotrophs in tan). Note that lichenized fungi are included to show that these orders have known genera even though they are not plant-associated. Guild data are from FUNGuild (Nguyen *et al.*, 2016) and genus-to-order matching is from Index Fungorum (http://www.indexfungorum.org). The tree topology was constructed manually following Hinchliff *et al.* (2015) and Open Tree of Life (https://tree.opentreeoflife.org/opentree/opentree10.4@ott352914/Fungi). The phylogeny is order level and branch lengths are not time calibrated. Agar, Agaricomycetes; Asco, Ascomycota; Basi, Basidiomycota; Chyt, Chytridiomycota; Dika, Dikarya; Doth, Dothideomycetes; Euro, Eurotiomycetes; Exob, Exobasidiomycetes; Glom, Glomeromycota; Kick, Kickxellomycotina; Leca, Lecanoromycetes; Leot, Leotiomycetes; Sord = Sordariomycetes. Taxa in Ascomycota are denoted in purple, Basidiomycota in blue and other clades in black. Note that genera absent from FUNGuild are absent from the bar chart (i.e. appear white) and proportional diversity within those orders does not tally to 1.

(5) Targeted examples

As our trait databases grow, it is important to consider how we want them to expand. Below we provide two targeted examples of trait types (gene copy number and colour) that vary in ways that appear to affect fungal function across guilds.

(a) *Genotype–phenotype connections across fungal guilds*

Fungal genomes can harbour evidence of species' guild associations. For example, saprotrophic fungi that rely on decomposition of dead plant matter for their carbon resources have high abundances of genes coding for plant carbohydrate-active enzymes (CAZys) in their genomes

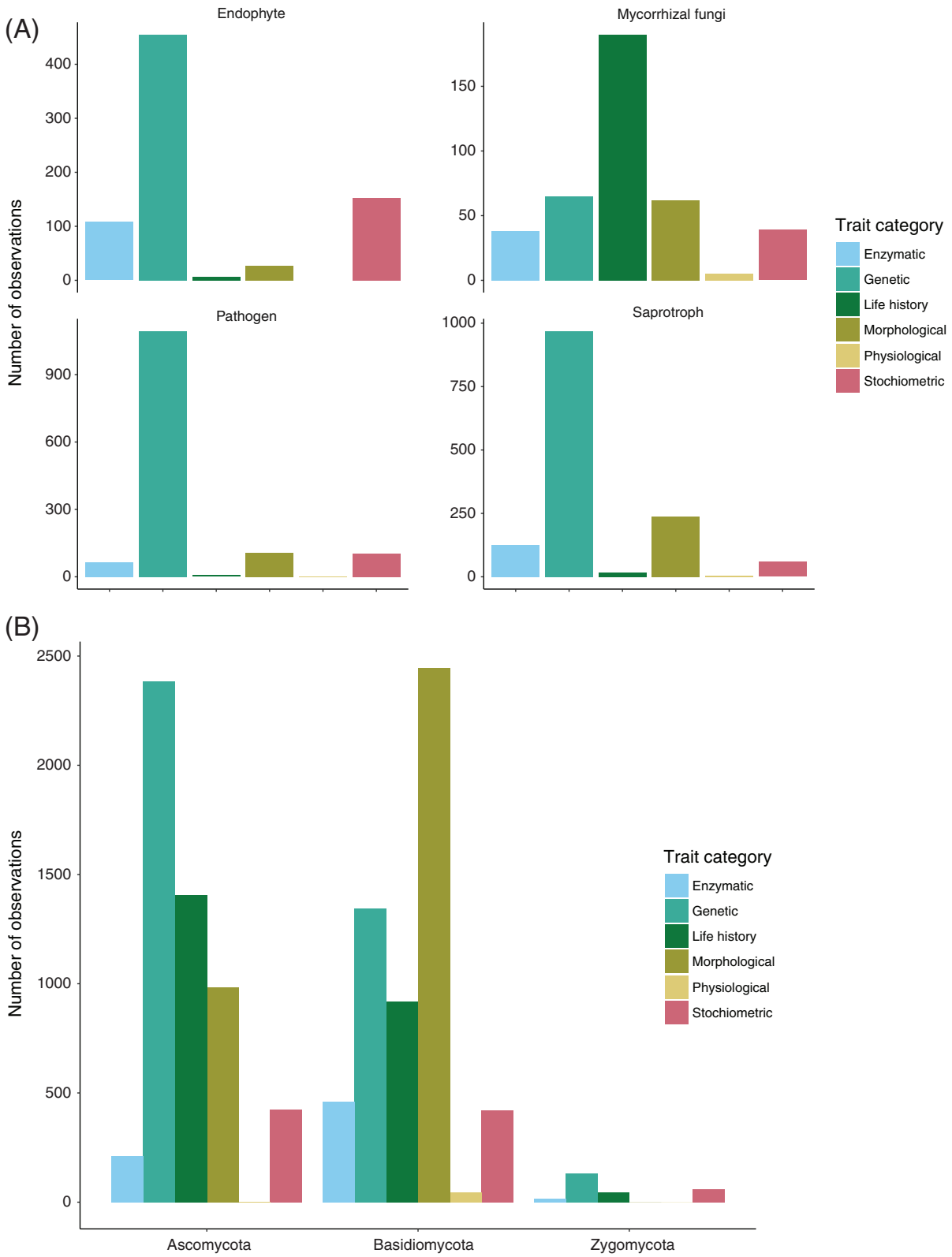

Fig. 5. Number of observations present in the Fungal Functional Trait Database (Fun^{Fun}) by (A) plant-associated fungal guilds (endophytes, mycorrhizal fungi, pathogens, and saprotrophs) from FUNGuild (Nguyen *et al.*, 2016) and (B) higher clades (Ascomycota, Basidiomycota, and Zygomycota). Bar plots represent trait categories with traits pooled into enzymatic (light blue), genetic (aqua), life history (green), morphological (brown), physiological (tan), and stoichiometric (pink).

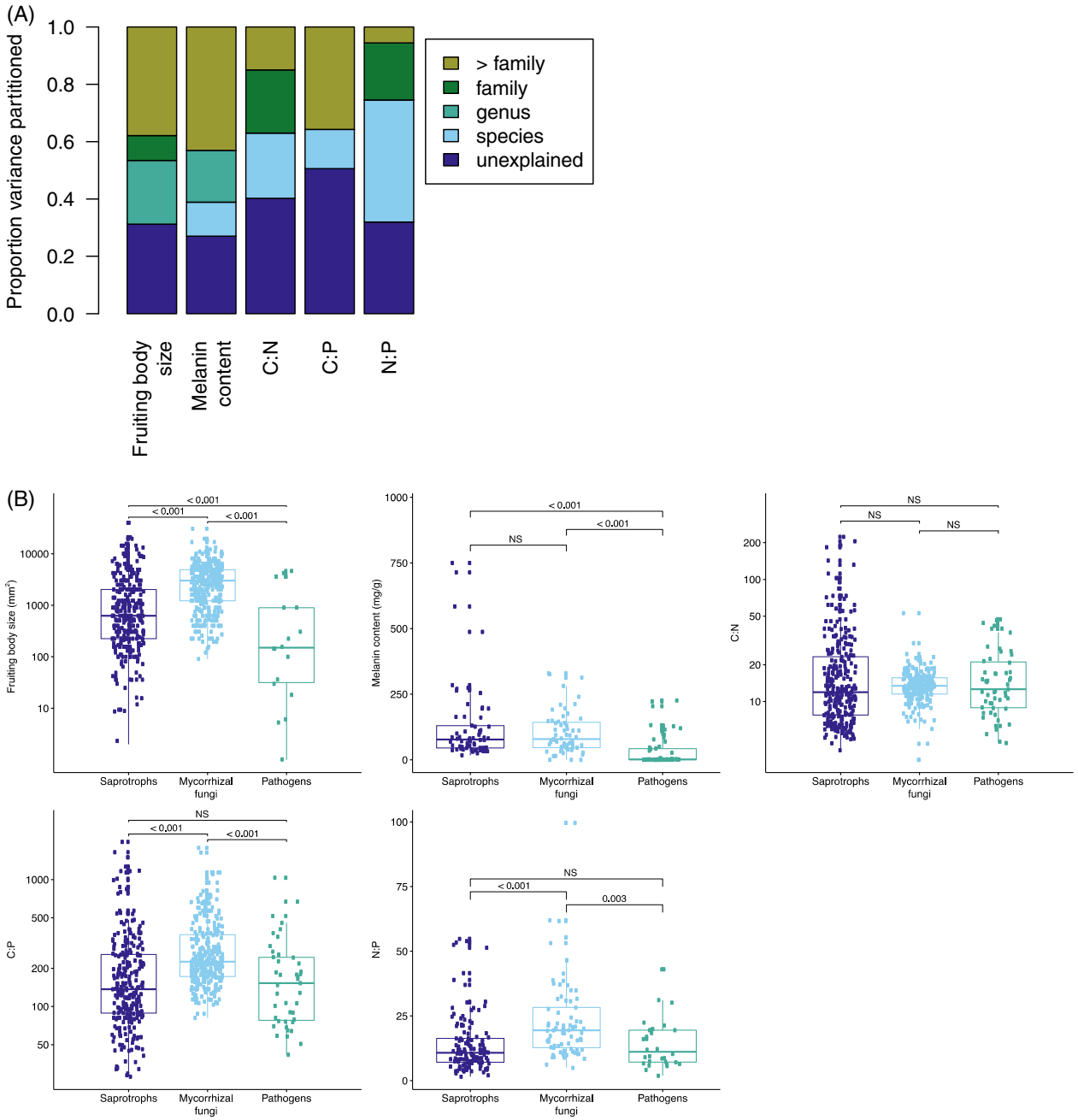

Fig. 6. Trait variation (A) partitioned to taxonomic levels and (B) compared across fungal functional guilds (saprotroph, pathogen, and mycorrhizal) for five fungal traits for which we have the most data: fruiting body size ($N = 690$), tissue melanin content ($N = 205$), and ratios of carbon (C), nitrogen (N), and phosphorus (P) ($N_{C:N} = 646$, $N_{C:P} = 743$, $N_{N:P} = 296$). Variance components in A were estimated as nested random effects (i.e. taxonomically nested clades including above family, family, genus and species) from linear models using the 'lme4' package version 1.1–17 (Bates *et al.*, 2015) in 'R' version 3.5.0 (R Core Team, 2018). Each random effect represents the proportion of variation that is explained by differences among groups at that taxonomic level, while 'unexplained' represents the residual variation (equal to 1 – conditional R^2; Nakagawa & Schielzeth, 2013). In B, raw data (small points) and boxplots are grouped by functional guild to demonstrate the distribution of trait values observed in the Fungal Functional Trait Database (Fun^{Fun}). Differences among guilds in the central tendency were compared using one-way analysis of variance for overall models and Tukey's honestly significant difference test for pairwise comparisons, except for melanin content, which was not log-normally distributed. Melanin content was compared using a Kruskal-Wallis test for an overall model and a Wilcoxon signed-rank test for pairwise comparisons. Results for overall models were: fruiting body size: $R^2 = 0.04$; $P < 0.001$; melanin content: $KW\ X^2 = 122.9$, $P < 0.001$; C:N: $R^2 = 0.03$, $P = 0.35$; C:P: $R^2 = 0.03$, $P < 0.001$; N:P: $R^2 = 0.10$, $P < 0.001$. Significance for all pairwise comparisons are noted in the figure.

(Fig. 7A). Mycorrhizal fungi, by contrast, must associate closely with live plants, as they acquire most of their carbon resources directly from the plant (Smith & Read, 2008). As a consequence, most mycorrhizal fungal guilds have lost the capability to produce certain types of CAZys related to a saprotrophic lifestyle (Kohler *et al.*, 2015). Fungi in the plant pathogen guild have high copy numbers of genes coding for CAZys, similar to saprotrophs, yet certain CAZys (such as the hemicellulose-degrading β-xylosidase enzyme) seem particularly high in plant pathogens (Fig. 7B), suggesting that most of the fungi identified as plant pathogens follow a more necrotrophic than biotrophic strategy (see Section V.2; Spanu *et al.*, 2010). Interestingly, fungi that are pathogenic on both plants and animals have some common genomic features, including high copy numbers of genes coding for chitinases, phosphate transporters, and polyketide synthases that produce melanized hyphal tissue (Fig. 7C). We note that copy number does not necessarily equate to expression levels (Eichlerová *et al.*, 2015); however, persistently high numbers across a number of species of the same guild suggests selection for those high numbers. With the increasing number of available fungal genomic and other -omic information generated and annotated through initiatives such as the 1000 Fungal Genomes Project (Grigoriev *et al.*, 2011, 2014), we will refine which gene families are inflated in connection with certain lifestyles, as well as detect other changes – beyond gene copy number variation – that are connected to shifts in fungal lifestyles.

(*b*) *Colour as an understudied trait of fungi*

Fungi exhibit extensive variation in colouration as can be seen by exploring quantitative metrics for colour traits for soil fungi in culture (Fig. 8A,B) and arbuscular mycorrhizal spores (Fig. 8C,D). Variation in spore colouration in some fungi can be heritable but also plastic, presumably in response to environmental cues (Bentivenga, Bever, & Morton, 1997). Striking variation is observed among fruiting bodies produced by various Basidiomycota and Ascomycota species but surprisingly few hypotheses have been put forward to explain the ecological significance of this variation, with those proposed largely being linked to advertising their toxicity (Sherratt, Wilkinson, & Bain, 2006). Pigments in the mycelium can enhance fungal fitness under stressful conditions (Fernandez & Koide, 2013), as well as having effects on ecosystem processes following fungal death (Fernandez & Kennedy, 2018).

Most work on fungal pigments is applied. Fungi have been used to dye textiles dating back to at least the 15th century in Europe (Bechtold & Mussak, 2009), and the practice is still in use today. For instance, instructional guides are available for dying wool with fungi, including the selection and preservation of dye-containing fungal species (Bessette & Bessette, 2001). There exist several published studies of the range of colours obtained by dyeing wool with different species of fungi using different solvents (Cedano, Villaseñor, & Guzmán-Dávalos, 2001). These pigments are associated with various characterized phenolic compounds, including lecanoric acid, derived from lichens in the genus *Roccella*, and atromentin, derived from fungi in the genera *Boletus* and *Paxillus* (Bechtold & Mussak, 2009).

Multiple other chemical compounds are commonly cited as responsible for ecologically relevant variation in fungal colour, but few have been studied in such a way that ecological function could be confirmed. Melanin (brown through black to dark-green) plays a protective role for fungi including tolerance of environmental stresses such as ionizing radiation (Jacobson, Hove, & Emery, 1995) and drought (Fernandez & Koide, 2013), infection and virulence for parasitic fungi (Gómez & Nosanchuk, 2003), and heat capture by pigmented yeasts (Cordero *et al.*, 2018). Various carotenoids (yellow through orange to red) are useful taxonomic characters among species within genera across a wide range of fungi (Valadon, 1976), and genes that allow the pea aphid (*Acyrthosiphon pisum*) and two-spotted spider mite (*Tetranychus urticae*) to produce carotenoids are hypothesized to have been acquired from fungi (Moran & Jarvik, 2010; Altincicek, Kovacs, & Gerardo, 2012). However, despite the observation that carotenoid biosynthesis was observed to increase in *Fusarium fujikuroi* following exposure to light (Estrada & Avalos, 2008), few studies of functional roles of these compounds have been conducted. In addition, few studies exist that examine how colouration traits link to climate and biogeography (Andrew *et al.*, 2016; Cordero *et al.*, 2018) or trade off with other traits related to fungal life histories or growth strategies (Kauserud *et al.*, 2011).

III. LINKING FUNGAL DIVERSITY TO TAXONOMIC NAMES WITHIN SYSTEMATIC HIERARCHIES

Understanding fungal functional ecology and evolution through the lens of trait variation requires compiling trait data, typically from numerous sources. To link data across databases and ask questions about fungal function, it is critical to use names within these databases that conform to a common taxonomy with uniform clade names. Here, we examine the progress and challenges of finding and describing fungal diversity.

(1) From molecules to species: assessing and describing fungal diversity

DNA sequencing has revolutionized fungal diversity assessments, with the potential to enhance collection and annotation of trait data. Many fungal species cannot be isolated and/or grown in culture, meaning that culture-based assessments overlook true diversity (O'Brien *et al.*, 2005; Arnold *et al.*, 2007; Tedersoo *et al.*, 2010; Siddique, Khokon, & Unterseher, 2017). HTS has become the go-to tool for fungal surveys from environmental samples; however, data generated also pose challenges, including incorporating abundance, depending on the type of HTS, as well as accurate species delineation and taxonomic assignment

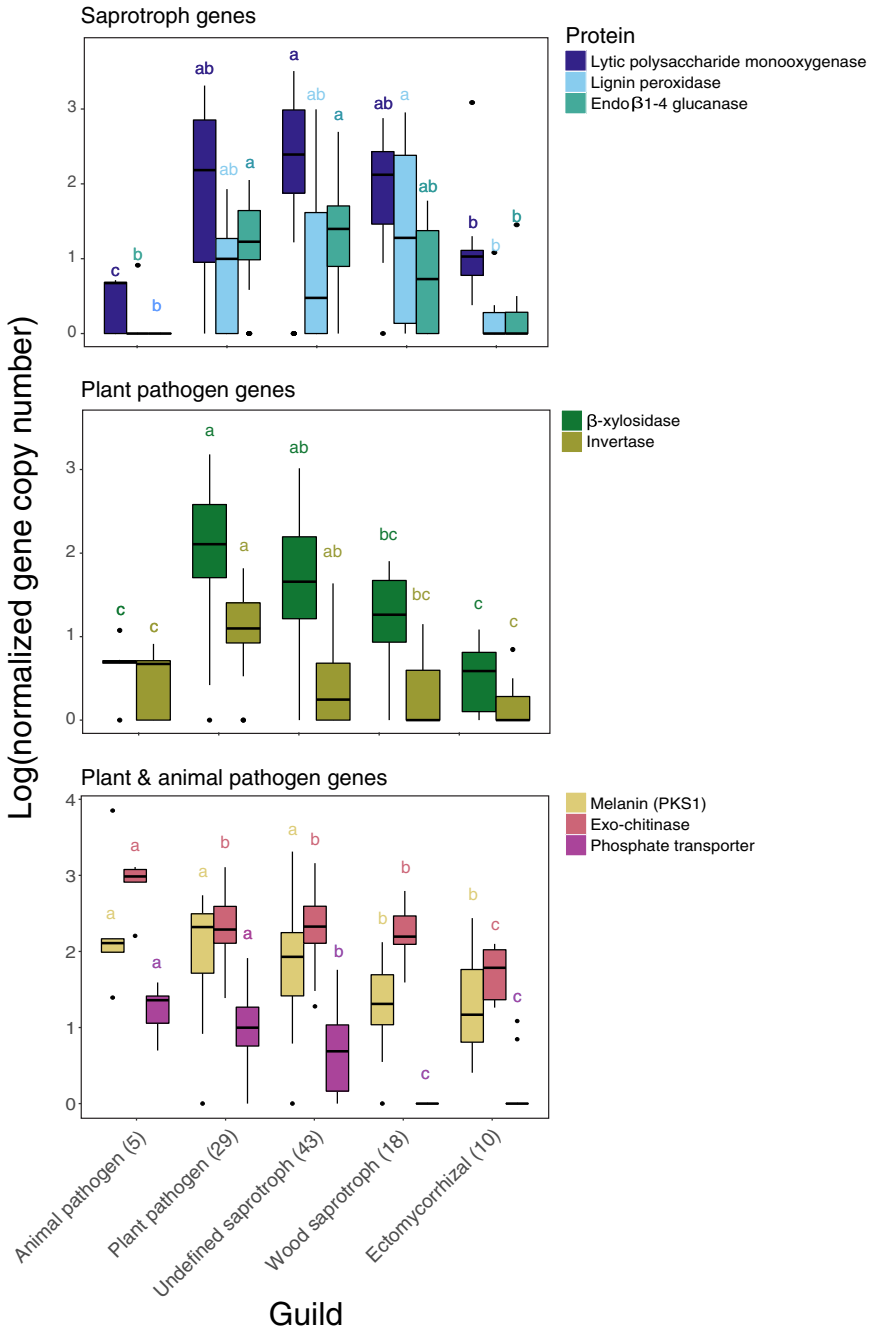

Fig. 7. Normalized copy numbers of genes coding for key proteins in saprotroph, plant pathogen, and plant and animal pathogen lifestyles across fungal guilds [animal pathogens, plant pathogens, undefined saprotrophs, wood saprotrophs, and ectomycorrhizal fungi from FUNGuild (Nguyen *et al.*, 2016)]. Note that animal pathogens are included for comparison with plant pathogens. Copy numbers were calculated for complete annotated, published genomes of 157 fungal species. Only guilds represented by more than one species with a fully sequenced genome were used in the analysis. Protein domain annotations (Pfam assignments) are assigned to protein domains based on their conserved function for protein-coding genes in each genome (El-Gebali *et al.*, 2019). Pfam domain annotations for protein-coding genes in each genome (Huntemann *et al.*, 2016) were downloaded from the Joint Genome Institute's MycoCosm web portal (Grigoriev *et al.*, 2014). Gene copies were calculated per 10,000 genes, following Treseder & Lennon (2015). Box mid lines show median values, box edges show data in the 1st and 3rd quartiles (25th and 75th percentiles), and whiskers show values that are at maximum 1.5 9 IQR from the edges (where IQR is the inter-quartile range, or distance between the first and third quartiles). Values are calculated as the average normalized gene count per genus (105 total) within a guild. Total genera included in each guild are reported in parentheses on the *x*-axis ($N = 5–43$). Statistical results are reported from a one-way analysis of variance for each gene with fungal guild as the independent variable. Letters represent significant ($P < 0.05$) differences among guilds in gene copy numbers using Tukey's honestly significant difference test for pairwise comparisons.

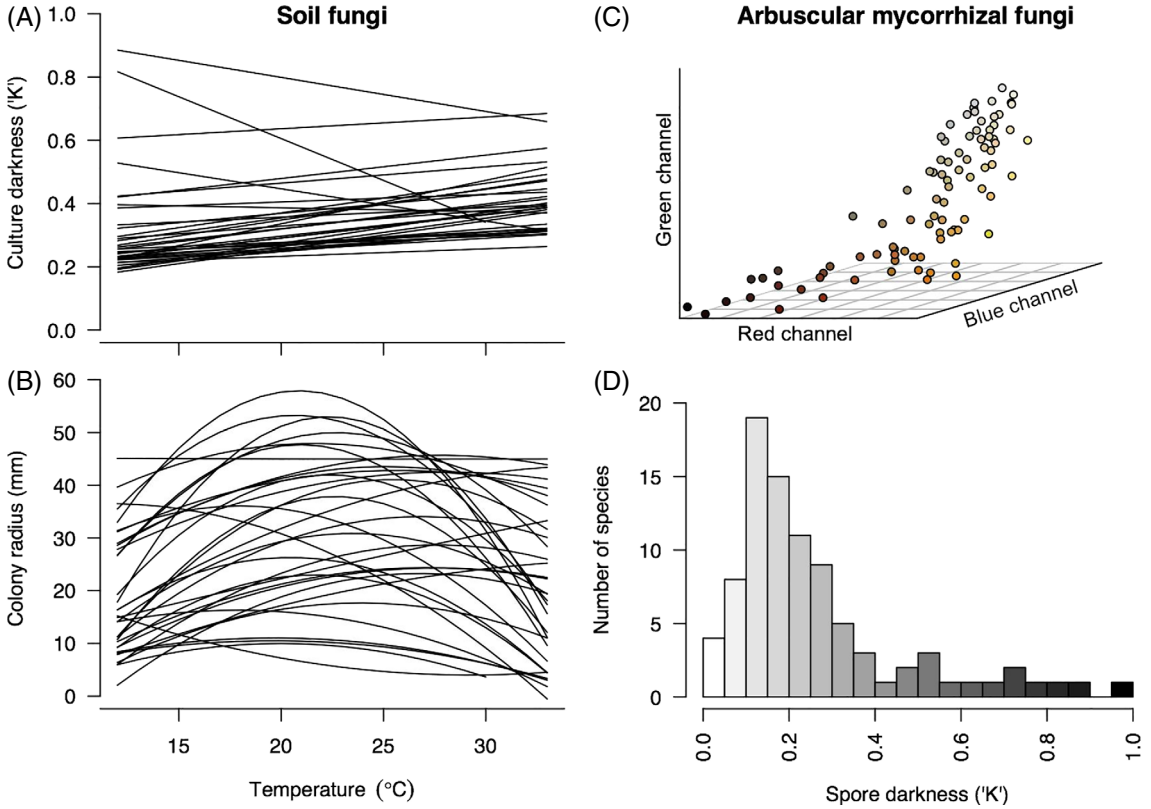

Fig. 8. Fungi isolated from soil and grown at increasing temperatures exhibit darker phenotypes (A) and variable growth responses (B). Each line represents a relationship for a single isolate; in A, the slope is positive for most isolates, as is the overall relationship. (C) Variation in spore colour for 69 species of arbuscular mycorrhizal (AM) fungi; colour is represented along three axes on the Red–Blue–Green (RGB) scale (based on the human perception of colours), each of which ranges from 0 to 255 and was obtained from images of spores on a black background, posted on the website of the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (http://invam.wvu.edu/). This variation can also be expressed along a gradient of light to dark phenotypes (D).

(Tedersoo *et al.*, 2010; Bazzicalupo, Bálint, & Schmitt, 2013; Lindahl *et al.*, 2013). For instance, many taxa and even large lineages are absent from our barcode databases, making fungal name assignments a particularly difficult problem. As such, traditional sampling and sequencing conducted in parallel with environmental HTS can provide more comprehensive views of fungal diversity (Arnold *et al.*, 2007; U'Ren *et al.*, 2014; Baptista *et al.*, 2015; Carbone *et al.*, 2017; Christian, Whitaker, & Clay, 2017; Truong *et al.*, 2017; Chen *et al.*, 2018).

Whereas many fungal species have only been detected through sequencing, other described species remain unsequenced (Bruns, White, & Taylor, 1991; Bruns *et al.*, 1992; Xu, 2016; Yahr, Schoch, & Dentinger, 2016). Therefore, environmental sequences belonging to these species cannot be attributed to them, leaving large gaps in linking different data streams. Efforts are needed to deposit and curate sequence data from type material into public databases (Abarenkov *et al.*, 2010; Nagy *et al.*, 2011; Osmundson *et al.*, 2013; Nilsson *et al.*, 2014; Schoch *et al.*, 2014). Assignment of environmental DNA sequences to known taxa or their proposal as novel lineages is imperative for effective communication among scientists (Nilsson *et al.*, 2016). Furthermore, as trait and guild assignments of databases such as Fun[Fun] and FUNGuild rely on accurate taxonomic assignments for fungal sequences, in addition to the need to curate existing sequence reference databases (Nilsson *et al.*, 2006), users must also carefully quality control their input data.

(2) Current state of the fungal tree of life

Despite various hurdles, not least an unwieldy diversity of largely unknown fungal species, mycologists have been building a classification that reflects evolutionary relationships (Hibbett *et al.*, 2007, 2018; Schoch *et al.*, 2009; McLaughlin & Spatafora, 2014; Spatafora *et al.*, 2016; Tedersoo *et al.*, 2018). Developing and refining this classification is critical for predicting clade properties including shared history of ecological guilds and functional traits. The most recent effort to build a comprehensive fungal tree of life that includes all recognized species was conducted by the Open Tree of Life project (https://blog.opentreeoflife.org). An important innovation was synthesizing information from published phylogenies and taxonomic classifications including taxa never before incorporated into phylogenies (Hinchliff *et al.*, 2015). Currently, however, the fungal tree,

although taxonomically comprehensive, is highly unresolved including numerous redundant names. In the future, as our phylogenetic resolution and coverage increase, we can link names on these phylogenies to other databases. Such linkages provide a framework for asking questions related to character evolution, evolutionary dynamics of host switches, and acquisition of virulence or pathogenicity, among others.

IV. FUNGAL GUILD ASSIGNMENTS

HTS has also increased our ability to collect environmental samples and assign taxa into ecological guilds (Nguyen *et al.*, 2016). Historically, different researchers concentrated on specific guilds, with limited work on inter-guild dynamics. Although this approach has been helpful in building knowledge (see Section V), it has provided limited ecological inference about the full ecosystem impacts of a given species, potentially shaped by cross-guild interactions. For example, it is known that interactions between certain mycorrhizal fungi and leaf litter saprotrophic fungi play key roles in determining rates of litter decomposition in forests (Gadgil & Gadgil, 1971, 1975).

Assigning species to guilds holds promise for synthesizing knowledge, but accurate guild assignment is not always straightforward. We often cannot observe taxa; additionally, some species can be placed in more than one guild. For unseen taxa, it may be possible to use taxonomic information for assignments. Ecological function is rarely conserved at high taxonomic levels within fungi (Fig. 4), but guild assignment often becomes more reliable at low taxonomic levels. For example, all known species in the genus *Russula* are ectomycorrhizal, and all known species in the genus *Puccinia* are plant pathogens. However, exceptions to ecological guild conservation among species within a genus, within a species, and even within an individual, are increasingly recognized. Examples of guild-shifting individuals are found among necrotrophic pathogens, which kill their host and live as saprotrophs on dead plant material (Olson *et al.*, 2012). Similarly, many endophytes are isolated from healthy plant tissues, but are also widely distributed as saprotrophs (Promputtha *et al.*, 2007; Voříšková & Baldrian, 2013; Martin *et al.*, 2015; Kohout *et al.*, 2018). Indeed, the genetic model organism *Neurospora crassa* can switch rapidly among pathogenic, saprotrophic, and endophytic lifestyles, enabling it to track changing environments (Kuo *et al.*, 2014).

An outstanding question for variable taxa is whether guild shifts equate to shifts in functional trait space. Understanding the evolutionary history of lineages may inform our understanding of what traits are necessary for guild changes. For example, *Metarhizium* and *Beauveria* are insect pathogens that are also found as endophytes and are related to the grass endophytes *Claviceps* and *Epichloë*; together they are believed to share a plant-associated common ancestor (Spatafora *et al.*, 2007; Barelli *et al.*, 2016; Christian *et al.*, 2017). *Metarhizium* and *Beauveria* have retained numerous genes for plant-degrading enzymes, perhaps making them particularly well suited to colonize plant hosts (Gao *et al.*, 2011). Additionally, brown rot fungi have evolved multiple times from white rot ancestors in Agaricomycotina in the Basidiomycota, coinciding with profound gene losses and shifts to non-enzymatic mechanisms (i.e. the Fenton reaction) for breaking down complex carbon compounds such as lignin in wood (see Section V.3; Martinez *et al.*, 2009; Eastwood *et al.*, 2011; Floudas *et al.*, 2012; Nagy *et al.*, 2017). Combining efforts from various databases (e.g. Figs 3–7) will be an asset to the scientific community; integrated data can shed light on areas for further research and emerging topical questions, such as the extent to which multi-guild membership is the exception or the rule, how guild membership is retained from common ancestry, and how variation in trait values is associated with specific guilds.

Building on this, it remains unclear why certain guilds are largely restricted to particular clades, whereas others appear numerous times across the fungal tree of life. It is likely that the ability of a lineage to transition among different guilds depends on the gains and losses of the traits underpinning that lifestyle (Varshney *et al.*, 2016). For instance, ectomycorrhizal fungi have evolved numerous times from saprotrophic ancestors, retaining genes to invade host tissue but often losing genes to break down more complex carbon compounds (Martin *et al.*, 2016). Additionally, transitions between certain guilds may be more likely than others. Arnold *et al.* (2009) showed, within the Ascomycota, that transitions between endophytes and pathogens were most common whereas transitions from endophytes to saprotrophs were more common than the reverse. The rare transitions suggest a limit or constraint on that particular evolutionary change and also create phylogenetic structure in the ecology of today's extant organisms. However, the rarity of the transition itself makes studying this area difficult (Uyeda, Zenil-Ferguson, & Pennell, 2018). Nonetheless, as trait databases grow and we construct a more comprehensive fungal phylogeny, we can begin to examine how coordination in evolutionary transitions varies between traits and guilds across the fungal branch of the tree of life.

V. FUNGAL TRAIT KNOWLEDGE: GUILD OVERVIEWS

Here, we discuss how a trait-based approach can enhance our understanding of fungi for four major guilds of plant-associated fungi: endophytes, pathogens, saprotrophs, and mycorrhizal fungi (Nguyen *et al.*, 2016). Each of these is represented in the FUN^{Fun} database, and we discuss insights emerging from this unique trait database.

(1) Endophytes

Endophytes are predominantly Ascomycota, occurring in all living land plant tissues without causing symptoms of disease (Wennstrom, 1994; Wilson, 1995; Saikkonen *et al.*, 1998; Stone, Bacon, & White, 2000). They are separated

into those transmitted from parent to offspring *via* the seed (vertically transmitted) *versus* among co-occurring plants or *via* the surrounding environment (horizontally transmitted). Vertically transmitted clavicipitaceous grass endophytes form a monophyletic group. They provide numerous benefits to plants, including deterring herbivory by producing toxic secondary metabolites (Clay, 1988) and enhancing drought tolerance (Kane, 2011) and nutrient uptake (Malinowski, Alloush, & Belesky, 2000). These effects have important consequences for host plants and their communities; for example, they can bias sex allocation (Gorischek *et al.*, 2013), facilitate host range expansion (Afkhami, McIntyre, & Strauss, 2014), suppress forest succession (Rudgers *et al.*, 2007), negate productivity–diversity relationships (Rudgers, Koslow, & Clay, 2004), and alter plant, herbivore, predator, and decomposer community compositions (Lemons, Clay, & Rudgers, 2005; Finkes *et al.*, 2006; Afkhami & Strauss, 2016).

Non-clavicipitaceous endophytes are taxonomically diverse, horizontally transmitted, and provide numerous benefits to host plants (reviewed by Rodriguez *et al.*, 2009). For example, endophytes from the major fungal phyla Basidiomycota and Ascomycota promote plant growth (Verma *et al.*, 1998; Newsham, 2011; Waqas *et al.*, 2015), confer abiotic stress tolerance (Redman *et al.*, 2002; Márquez *et al.*, 2007; Sherameti *et al.*, 2008), and modulate host plant defence (Usall *et al.*, 2000; Busby, Peay, & Newcombe, 2016*a*). However, not all interactions with endophytes are beneficial; many form commensal relationships with hosts, where they access host resources with little apparent impact on their hosts (May, 2016). They can even be latent pathogens or saprotrophs, changing their functional guild in response to cues from the environment or host.

A trait-based approach may provide a quantitative framework to predict ecological differences defining particular species (Gazis *et al.*, 2016; Christian *et al.*, 2017). Both ability to exist as and ecological impacts conferred by endophytes are polyphyletic within fungi, and taxonomic identity alone provides little information about the evolutionary history and ecology of most endophytes (notable exceptions include the clavicipitaceous grass endophytes and *Piriformospora*; Verma *et al.*, 1998). Critical traits may be detected through identifying molecular shifts (e.g. the presence and expression levels of certain genes) among species (Fig. 7). For instance, the capacity to produce plant-degrading enzymes, or to silence plant defence pathways, may be needed to colonize plant tissues successfully. Additionally, progress in understanding endophyte function is likely to occur through molecular tools. The ability to produce certain chitinases may underpin mycoparasitism, leading to endophytes antagonizing pathogens thereby suppressing plant diseases, whereas the ability to produce gibberellin may allow for plant growth promotion in endophytes (Waqas *et al.*, 2015).

Although traits can determine which and how fungi exist as endophytes, a trait-based approach by itself may be incomplete for decoding when and where endophytes confer particular ecological functions, given the degree of context dependency in plant–endophyte symbioses (Adame-Álvarez, Mendiola-Soto, & Heil, 2014; Busby, Ridout, & Newcombe, 2016*b*). For example, priority effects can have important consequences for pathogen suppression by endophytes; inoculating a wild lima bean (*Phaseolus lunatus*) with endophytes inhibits pathogenic *Pseudomonas* spp. if inoculated first but facilitates disease if the pathogen colonized the plant first (Adame-Álvarez *et al.*, 2014). More broadly, it is common for fungi isolated from asymptomatic healthy hosts in one study to be reported as plant pathogens on another host in a different study (Christian *et al.*, 2016). Even within well-studied Clavicipitaceae, fungal species occupy a diversity of functional roles across a pathogen-to-mutualist spectrum; some differences may be predicted by traits such as transmission mode (horizontal *versus* vertical) and host specificity (Christian *et al.*, 2017). Additionally, manifestation of a pathogen *versus* endophyte strategy is dependent on the susceptibility of host individuals to that fungus; this is another example of how a strategy is the outcome of both traits of the plant and fungus. Manipulative experiments in combination with a trait-based approach in which we explicitly test for context-dependent shifts will facilitate our understanding of both identity and what they are doing as endophytes.

(2) Pathogens

Pathogenic fungi occur throughout the fungal evolutionary tree; however, the majority of described fungal plant pathogens fall into Basidiomycota and Ascomycota. Ascomycota is particularly rich in pathogens with most major clades containing plant pathogens (Berbee, 2001). Within the Basidiomycota, Pucciniomycotina and Ustilaginomycotina contain numerous plant pathogenic species of economic and ecological importance. Additionally, many Basidiomycota pathogens (especially forest pathogens) can be found in Agaricomycotina (Sinclair & Lyon, 2005).

Pathogens have important effects on host fitness, community structure, and ecosystem function. To be considered pathogenic, a fungus has to infect host tissue and induce disease or damage, meaning it impairs normal functioning and reduces plant fitness. While fungal pathogens are responsible for the population collapse of several animal species, notably amphibians and bats (Fisher *et al.*, 2012), the highest diversity of pathogenic fungi is associated with plants (Agrios, 1997). Infection can result in increased crop mortality, posing threats to food security (Dean *et al.*, 2012) and ecosystem function. Plant pathogens can also play a positive role in natural ecosystems by limiting dominance of a given taxon and promoting plant diversity (Maron *et al.*, 2011).

Despite being relatively well characterized in their phylogenetic distribution, three major challenges remain for ascribing fungal taxa to the pathogenic lifestyle. First, most pathogenic fungi can shift to other functional groups, particularly saprotrophs and endophytes (see Section V.1). Second, virulence (i.e. severity of reduction in host fitness) of a particular fungus can vary depending on host species and environment (see discussion of context dependency in Sections V.1 and V.3). For instance, changes in local climate can increase severity of damage (Fisher *et al.*, 2012). Third,

most pathogenic fungi have been described on plant hosts of human interest, particularly agroecosystems, meaning we are uncertain whether these fungi behave as pathogens in natural communities. A trait-based approach is well suited to address these challenges. Specifically, from an ecological perspective, fungal traits may be used to predict the: (1) likelihood a species will behave as a pathogen; (2) host range; (3) virulence; and (4) conditions under which host fitness is reduced.

For example, nutritional strategy, can be informative in predicting the ecology of pathogens. Nutritional strategy variation is underpinned by differences in enzymatic arsenals (Ohm *et al.*, 2012). Pathogens can be separated into biotrophic, necrotrophic, and hemibiotrophic. Biotrophs use resources from living tissues, necrotrophs from dead tissues and hemibiotrophs from both living and dead tissues (Amselem *et al.*, 2011). Knowing which enzymes a given pathogen can produce allows us to predict how that pathogen invades plants (e.g. *via* enzymes for carbohydrate degradation in cell walls; Fig. 7A; Nagy *et al.*, 2017) and overcomes host defence responses (Plett & Martin, 2011). Biotrophs have the most extreme host dependency (Zhao *et al.*, 2013), which has resulted in the development of special morphological traits for nutrient uptake from living tissue, a reduction in number of cell wall degrading enzymes, and complex metabolic pathways to overcome host resistance (Mendgen & Hahn, 2002). This correlation of traits makes this group less likely to switch to other functional groups (such as saprotrophs or endophytes). By contrast, necrotrophs and hemibiotrophs rely on enzymes for carbohydrate degradation for both plant death and nutrient uptake (with some exceptions in necrotrophs that kill host tissue *via* toxins; Mengiste, 2012)) (Fig. 7). Similar carbohydrate-degrading enzymes are reported in saprotrophs (Nagy *et al.*, 2017), which explains in part the extensive species overlap among these groups (Fig. 7A; Gazis *et al.*, 2016). In fact, many saprotrophs have been considered necrotrophs affecting weak hosts (e.g. at seedling or senescent stages; Thomma, 2003; Jarosz & Davelos, 2006). Furthermore, it is increasingly recognized that some necrotrophic fungi only cause disease in a few hosts, but infect other host plant species asymptomatically as endophytes. A better understanding of coordination and tradeoffs among traits, such as the presence, copy number and expression levels of genes coding for such enzymes (Gazis *et al.*, 2016), could delineate when, why, and how particular hosts and environmental conditions trigger a pathogenic *versus* endophytic or saprotrophic lifestyle (Fig. 7).

(3) Saprotrophs

Saprotrophy is not phylogenetically conserved, as it is found across all major lineages of fungi. However, certain types of plant saprotrophs can be assigned to specific taxonomic groups, particularly wood-decomposing fungi, which are restricted to Dikarya. For example, white rot fungi (capable of degrading significant amounts of lignin) are found primarily, but not exclusively, in Agaricomycetes in the Basidiomycota where they are widespread, whereas brown rot fungi (capable of degrading select carbohydrates, with minimal lignin removal) are restricted to certain clades within Agaricomycetes and Dacrymycetes (Gilbertson, 1980). Leaf-litter decomposing fungi come from similar phylogenetic lineages as those that decay deadwood (Osono, 2007; Talbot *et al.*, 2015), a trend that holds for terrestrial and aquatic species (Bärlocher, 2016), but soil saprotrophs are found within all major lineages of fungi, including early diverging lineages, as well as Dikarya.

Across terrestrial and aquatic ecosystems, saprotrophs degrade dead organic matter, including the most abundant components: wood, leaf litter, and soil organic matter. These fungi are biochemical engineers, recycling immense pools of carbon and nutrients. They possess a range of enzymes (and non-enzymatic pathways) making them uniquely capable of degrading all structural components of dead plant material, including lignocellulose (Fig. 7; Baldrian *et al.*, 2011; Riley *et al.*, 2014; Eichlerová *et al.*, 2015; Schilling *et al.*, 2015; Nagy *et al.*, 2017; López-Mondéjar *et al.*, 2018). As wood and leaf litter pools degrade, they vertically stratify in terrestrial and aquatic systems, ultimately segregating saprotrophic communities over progressively decomposed material (Lindahl *et al.*, 2007; Lindahl & Boberg, 2008; Baldrian *et al.*, 2012; Richards *et al.*, 2012; Taylor *et al.*, 2014). Even though genes, enzymatic pathways, and evolutionary histories for lignocellulose processing are shared in fungi in soil and water (Hyde *et al.*, 2015), they can have striking contrasts in different environmental conditions such as oxygen availability.

Lignocellulolytic saprotrophs have been classified into different rot strategies, but there remain gaps in knowledge about genes, gene products, and functions that underpin these groupings. White and brown rot strategies are most common; however, soft rot can play important and underappreciated roles, including in aquatic systems (Gessner *et al.*, 2007; Hyde *et al.*, 2015; Kodsueb *et al.*, 2016). With HTS, we now realize binary distinctions between white and brown rot strategies are unsupported (Riley *et al.*, 2014; Nagy *et al.*, 2016); wood itself reveals a spectrum of carbohydrate *versus* lignin selectivity (Worrall, Anagnost, & Zabel, 1997; Schilling *et al.*, 2015). Additionally, brown rot fungi are polyphyletic, repeatedly emerging from white rot lineages in Agaricomycetes (see Section IV) and converging on similar mechanisms (i.e. the Fenton reaction) to decay wood (Kaffenberger & Schilling, 2015). Genes underpinning this reaction have yet to be determined (Zhang *et al.*, 2016).

A quantitative trait-based approach, e.g. knowledge of presence, copy number, and expression level of different decay genes (Fig. 7) and complex carbon compounds they can decay (López-Mondéjar *et al.*, 2018) can lead to a better understanding of how these fungi decompose different wood components. Such knowledge will predict the fate of reallocated wood carbon (e.g. released to the atmosphere as CO_2 or locked in soil as recalcitrant residues). These different pathways for carbon are driven by the decay capabilities of species colonizing wood and may be influenced by priority effects (Fukami *et al.*, 2010) initiated by endophytes

(Song *et al.*, 2017) or interactions with other fungi (Maynard *et al.*, 2017), bacteria (de Boer *et al.*, 2005) and invertebrates (Crowther *et al.*, 2015) in soil.

Known lignocellulotyic saprotrophs can also function as members of other guilds, even persisting in plant tissue as it transitions from living to dead (Voříšková & Baldrian, 2013; Kohout *et al.*, 2018). Secretomes vary across taxonomic and functional boundaries. Similar enzymes are shared between litter and deadwood saprotrophs (Osono, 2007; Eichlerová *et al.*, 2015; Talbot *et al.*, 2015), but litter saprotrophs also produce substrate-specific enzymes (Carreiro *et al.*, 2000; Sinsabaugh, Carreiro, & Repert, 2002; Talbot *et al.*, 2015), which degrade more labile carbon and are responsible for uptake of nutrients from litter, soil, and microbial necromass (Baldrian, 2009). Similarly, mycorrhizal fungi produce enzymes that degrade plant material (Talbot *et al.*, 2015) and may contribute to leaf and soil organic matter decay (Talbot, Allison, & Treseder, 2008; Shah *et al.*, 2016). Moving the emphasis from strictly defined groups (e.g. rot strategies) and guilds to functionally relevant comparisons of species traits will allow for an integrative consideration of how relative competitive abilities and environmental tolerances (Nordén *et al.*, 2013; López-Mondéjar *et al.*, 2018) of different fungal species shape community assembly (Maynard *et al.*, 2017) and the influence of these communities on plant decay.

(4) Mycorrhizal fungi

Mycorrhizae represent intimate associations between fungi and plant roots that are often beneficial to both partners. Both sides of the symbiosis are phylogenetically diverse. The mycorrhizal lifestyle is found in fungi in Basidiomycota, Ascomycota, and Mucoromycota (specifically the Glomeromycotina and Mucoromycotina). Mycorrhizae are typically categorized into four main strategies: arbuscular (AM), ecto- (EcM), ericoid (ErM), and orchid (OM), although other classifications exist (Smith & Read, 2008; Nagy *et al.*, 2017). These strategies are defined by plant–fungal interface structures produced within roots and, for some, the taxonomic affiliation of hosts (Smith & Read, 2008). Mycorrhizal symbioses are perhaps best known for their key role in driving terrestrial productivity, but they also improve water uptake in host plants (Brownlee *et al.*, 1983; Augé, 2001), alleviate heavy metal and salinity stresses (Jentschke & Godbold, 2000), and protect plants from pathogens (Whipps, 2004). Mycorrhizal fungi can significantly influence soil carbon dynamics (Wurzburger, Clemmensen, & Austin, 2018) by directly contributing soil organic matter (Rillig, 2004; Clemmensen *et al.*, 2013), as well as priming or inhibiting turnover of organic matter in soils (Hodge, Campbell, & Fitter, 2001; Fernandez & Kennedy, 2016, 2018) and possibly even influencing fire processes (Powell, Riley, & Cornwell, 2017).

Mycorrhizal types occupy different portions of trait space (Smith & Read, 2008), with considerable variability in traits, including intercellular interface with hosts, level of host dependency, hyphal diameter, septation, nutrients transferred and maximum extension lengths from roots (Smith & Read, 2008). Well noted axes of trait variation among mycorrhizal types relate to degree of access to organic *versus* inorganic nutrients, with most EcM, ErM and OM fungi having access to organic nutrients due to diverse enzyme suites, as compared to AM fungi, which are largely constrained to the uptake of inorganic nutrients (although see Hodge *et al.*, 2001). This distinction makes the distribution of mycorrhizal types among ecosystems generally predictable based on vegetation type and rates of organic matter turnover (Read, 1991; Steidinger *et al.*, 2019).

Whereas the fungal nutrient side of symbioses between plants and mycorrhizal fungi has received considerable focus (Phillips, Brzostek, & Midgley, 2013; Treseder *et al.*, 2018), a better understanding of traits associated with carbon movement between host and fungus requires attention. Studying trait variation within and across mycorrhizal types and linking it to traits associated with ranges of nutrients transferred, elemental stoichiometry, carbon source–sink dynamics (e.g. fungal respiration rates, extraradical hyphal density, and enzyme production), and biochemical mechanisms of resource exchange will enhance theories that explain resource trading and mutualism stability (Nehls *et al.*, 2007; Kiers *et al.*, 2011; Johnson *et al.*, 2015; Walder & van der Heijden, 2015; Powell & Rillig, 2018).

Using a trait-based approach also holds promise for providing new perspectives on the evolutionary dynamics of mycorrhizal symbioses. For example, AM is ancestral in land plants, and EcM has several independent evolutionary origins from, and reversals to, a facultative AM state (Maherali *et al.*, 2016). Speculation as to the sources of these evolutionary transitions focuses on plant-centric mechanisms. However, it may be that some AM fungal traits re-enforce the persistence of mycorrhizal states through evolutionary time (which may explain relatively infrequent transitions of plants to a non-mycorrhizal state; Maherali *et al.*, 2016). Furthermore, the conspicuous absence of reversals to saprotrophy by EcM fungi (Bruns & Shefferson, 2004) suggests that traits involved in transitions to root symbiotic lifestyles likely represent fixed transitions (Martin *et al.*, 2016).

Finally, from ecological perspectives, focus on quantification of mycorrhizal traits may provide important insights into the outcomes of fungal interactions. Niche differentiation among lineages of mycorrhizal fungi results in occupation of different habitats in space (e.g. root *versus* soil colonisation extent among AM fungal families; Powell *et al.*, 2009) and time (e.g. EcM exploration types shifting in prevalence during ecological succession; Peay, Kennedy, & Bruns, 2011). However, recent studies suggest mycorrhizal community assembly is still strongly dependent on interspecific interactions (Kennedy, Peay, & Bruns, 2009; Werner & Kiers, 2015; Powell & Bennett, 2016). Although traits linked to competition (particularly antibiosis) are well studied for saprotrophs, traits that explain variation in competitive outcomes among mycorrhizal fungi remain poorly studied. For instance, mycorrhizae compete to access nutrients from spatially and temporally ephemeral patches, involving tradeoffs between allocations to hyphal growth *versus* enzyme production (Moeller & Peay, 2016). Certain host species also

associate with both AM and EcM fungi, but each mycorrhizal type typically dominates at different host ages or ecosystem successional stages (Egerton-Warburton & Allen, 2001; Piotrowski *et al.*, 2008; Albornoz *et al.*, 2016). A focus on fungal traits and their associations with short-term (host development) and long-term (ecosystem succession and retrogression) environmental changes may determine whether this pattern is due to direct interactions between fungi in the two types, temporal variation in host-plant requirements facilitated by each type or tolerance of types to local environments.

VI. FUTURE DIRECTIONS FOR FUNGAL FUNCTIONAL ECOLOGY AND EVOLUTION

Above we provide a review of the current state of the literature on fungal functional ecology and complement this with initial analyses from a novel and growing fungal trait database. From both views, it is clear that many fungal taxa shift guild membership through time and context, providing an interesting emerging area of study for functional ecology. Additionally, our literature review highlights important functional differences within and among guilds. Many of these differences revolve around molecular and chemical shifts. In all cases, plant-associated fungi must invade hosts, meaning they need the enzymatic capacity to break down plant tissues, although whether these enzymes allow fungal colonizers simply to invade or degrade host tissues fully varies by guild. Furthermore, specific guilds need to overcome plant resistance to invasion by, for instance, silencing plant defence pathways, whereas other guilds, living mutualistically, produce beneficial chemicals for their host, e.g. plant hormones. Our preliminary database analyses similarly provide interesting differences among clades and guilds in several morphological and chemical traits.

Despite these advances, key knowledge gaps across various guilds and clades exist both in the literature and in our database (Figs 4 and 5), limiting the current extent of our understanding of fungal functional ecology and evolution. To fill these gaps, researchers with different specialties must continue to engage in dialogue. Such crosstalk will advance knowledge in one clade, guild, or discipline by looking at what has been done in another. For example, carbohydrate assimilation measures have had a long history in yeast-forming groups; such protocols could translate to studies of filamentous fungi in combination with emerging genomic data. Analyses across all fungi will be facilitated as we make accessible and consolidate data from numerous taxa together. Although targeted novel data collection is needed, in many cases gaps could be filled by digitizing existing non-electronic format resources (e.g. monographs for host ranges) or harvesting data from existing databases that contain, for example, information on fungal phenological traits (Miller & Bates, 2018). Adding studies and data on fungal function will improve the community's ability to compare across strategies (e.g. guilds) and clades.

The recent database revolution has generated a wealth of easily accessible information on organisms, communities, and ecosystems (Falster *et al.*, 2015); however, cross-referencing this cosmos is needed to achieve an accessible, integrative understanding of life on earth. One way to link across studies and databases is through fungal names, such as genera and species, which are shared among resources such as Fun^{Fun} and FUNGuild (Nguyen *et al.*, 2016). Although fungal taxonomy is in a state of flux, progress has been made in cataloguing and digitizing the names of fungal taxa, and these names are now routinely associated with Life Science Identifiers (LSIs), Universal Unique Identifiers (UUIDs), and registration numbers (Clark, Martin, & Liefeld, 2004; Redhead & Norvell, 2013). These provide a second way to link across databases. Use of these name identifiers, as well as assigning Digital Object Identifiers (DOIs) to individual database efforts or data items, along with providing application program interfaces (APIs), guarantees that information within databases is standardized, machine-readable, and accessible to researchers. These efforts facilitate cross-database communication and collaboration that promote synthesis, help in identifying gaps and increase discoverability of genetic, ecological, and evolutionary information. Furthermore, databases need to be dynamic in handling name information so that they can link to the most updated taxonomies; database overlaps will be maximized as they use the same taxonomies. Together, attention to these details increases data quality and ensures lifespan beyond individual efforts; however, an ongoing challenge will be to resolve taxonomic, sequence, trait, and guild information for individual entries.

As the trait databases grow, the community must consider data and metadata standards, as has been done within other communities (Wieczorek *et al.*, 2012; The Gene Ontology Consortium, 2015), as well as the potential for integration with systems (e.g. https://www.ebi.ac.uk/ols/index) that can provide a conceptual framework for traits. Because trait data are diverse there is no 'one size fits all' for how to standardize across all traits; however, it is imperative for metadata to be deposited with trait data so that end users can determine similarity among studies in a given trait (e.g. if experimental conditions differ). Open databases will ideally promote establishment of standards as data are shared and discussed in the community. Recommended protocols can be developed for fungi as has occurred, for instance, in plants (http://prometheuswiki.org; Pérez-Harguindeguy *et al.*, 2013) and macro fungi (Dawson *et al.*, 2019).

Concepts and tools developed here can be applied broadly beyond plant-associated fungi. As knowledge on fungal function in the literature and our database expands, this work can link with other existing databases, such as International Society for Human and Animal Mycology ITS Database (http://its.mycologylab.org/) and UNITE (https://unite.ut.ee/). From these, we will gain the ability to predict fungal traits and species distributions in understudied habitats, groups, and clades, potentially even extrapolating

out to other microbial clades (Hibbett *et al.*, 2016). This approach has utility for a range of other fungi, including those that are pathogens or mutualists of humans, are pathogens of insects, feed on nematodes and other invertebrate animals, and cause emergent wildlife disease epidemics. Additional trait data can refine predictions of host preference and likelihood of disease epidemics.

By synthesizing across databases, we can answer novel questions about the ecology and evolution of fungi. For example, how much of the taxonomic or functional diversity is variable in guilds? Similarly, as fungi shift across guilds, does trait space shift? As a dated fungal phylogeny becomes available, we will have the tools and knowledge to model the evolution of guild and trait transitions across the evolutionary history of fungi, link environment tolerances to traits, and determine which fungal traits have fitness consequences for hosts. Key gaps exist in our knowledge; however, consolidation of data into emerging databases advances us toward closing these gaps and provides a framework on which to build further. We also need to encourage researchers to take unconventional approaches in the selection of functional traits, such as the potential importance of colour (Fig. 8). We anticipate that the emergence of a trait-based approach to fungal biology will prove to be an exciting time in which to study the ecology of plant–fungal interactions.

VII. CONCLUSIONS

(1) In this review of fungal functional ecology, we examine what is currently known and unknown about plant-associated fungal guilds and how we can use a trait-based approach to advance our knowledge of these guilds.

(2) We define guilds based on the resource use of the members, discussing in turn endophytes, pathogens, saprotrophs, and mycorrhizal fungi. In our exploration, we note that guild is often conserved within a genus; however, there are examples of intra-generic, intra-specific and even intra-individual variation in guild membership. It is currently unclear how traits shift with these guild shifts.

(3) We argue that fungi are a tractable system to test outstanding ecological and evolutionary theory as: (*a*) individuals span from micro- to macro-scales; (*b*) they have measurable emergent traits with their plant hosts; and (*c*) they offer unique tools developed for industry but useful for basic science.

(4) By introducing a new fungal functional trait database (Fun^{Fun}) that includes data on genetic, enzymatic, morphological, stoichiometric, life history, and physiological traits and linking that to other databases (e.g. FUNGuild, Index Fungorum), we learn that for the traits with the most data, important differences occur in fruiting body size, stoichiometry and melanin among guilds.

(5) Building and adding to our and other databases require bringing different data sources to a common taxonomy. We describe the state of fungal taxonomy and systematics, including how the advent of HTS has revealed previously hidden diversity. However, a large proportion of fungal diversity still needs to be named and placed phylogenetically.

(6) There are numerous critical fungal traits, e.g. spore size, but many of the recognized traits that underpin different plant-associated guilds are chemical, e.g. enzymes and proteins; these chemical traits often exhibit intra-guild variation. Endophytes show important variation in enzymes and hormones, whereas pathogens often require enzymes for invading and overwhelming host defences. Saprotrophs use different decay enzymes to break down dead plant tissues, whereas mycorrhizal fungi sometimes access organic nutrients through excretion of enzymes. Additional knowledge of the presence, copy number, and expression levels of genes coding for these chemical traits will provide better insight into how different plant-associated fungi make their living.

(7) Finally, we end by suggesting how we can make progress in our efforts to understand fungal functional ecology and evolution. This includes contributing towards efforts to support fungal taxonomy and systematics, as well as the use of universal identifiers. For end users to best capitalize on growing databases, we should develop data and metadata standards. Resources developed here can be transferred to other guilds and clades (e.g. bacteria), opening the door to progress on the functional ecology and evolution of a previously hidden world.

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