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Finding fungal ecological strategies: Is recycling an option?

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ABSTRACT

High-throughput sequencing (e.g., amplicon and shotgun) has provided new insight into the diversity and distribution of fungi around the globe, but developing a framework to understand this diversity has proved challenging. Here we review key ecological strategy theories developed for macro-organisms and discuss ways that they can be applied to fungi. We suggest that while certain elements may be applied, an easy translation does not exist. Particular aspects of fungal ecology, such as body size and growth architecture, which are critical to many existing strategy schemes, as well as guild shifting, need special consideration in fungi. Moreover, data on shifts in traits across environments, important to the development of strategy schemes for macro-organisms, also does not yet exist for fungi. We end by suggesting a way forward to add data. Additional data can open the door to the development of fungi-specific strategy schemes and an associated understanding of the trait and ecological strategy dimensions employed by the world's fungi.

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1. Introduction

There are ~12 gigatons of fungal carbon in the world, containing ~200 times as much biomass as humans (Bar-On et al., 2018). This biomass is comprised of an unknown number of species, with typical estimates around 2–4 million (Hawksworth and Lücking, 2017) but some as high as 165.6 million (Larsen et al., 2017). Currently ~144,000 fungal species have been described (<https://stateoftheworldsfungi.org/>). These species are differentially distributed across the main branches of the fungal phylogeny: the bulk of diversity lies within Ascomycota (~62%) and Basidiomycota (~35%) with remaining diversity (~3%) spread across Mucoromycota, Zoopagomycota, Chytridiomycota, Blastocladiomycota,

Cryptomycota and Microsporidia.

While the origins and maintenance of so many species remain a mystery, we are gaining insight into how fungal diversity is distributed around the globe. Historically, it was believed that fungi were not dispersal limited, with any species able to reach any location, discussed in Peay et al. (2010) and Adams et al. (2013). However, additional sampling has revealed a large turnover of fungal taxa across geographical spaces and ecological settings (Green et al., 2004; Peay, 2007; Peay et al., 2010; Talbot et al., 2014; Powell et al., 2015; Hu et al., 2019; Steidinger et al., 2019). Additionally, emerging molecular tools, such as high-throughput sequencing (e.g., amplicon and shotgun), are uncovering incredible numbers of individuals, operational taxonomic units (OTUs) and/or species in small spaces (Kembel and Mueller, 2014; Tedersoo et al., 2014; Taylor et al., 2016; Egidi et al., 2019; Lee et al., 2019). This work complements early observations that a gram of soil can contain 10^5 – 10^6 fungal colony forming units (Waksman, 1922), and together these data suggest that we are surrounded by a rich and

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complex array of fungal taxa.

This diversity raises a number of questions including (1) Why do so many fungal species exist? (2) How can so many species coexist? (3) Are these assemblages assembled via deterministic (Chesson, 2000; Chase and Leibold, 2003) or neutral (Hubbell, 2001) processes? (4) If deterministic, which processes are most critical? In examining the processes underlying community assembly, it may be that fungal assemblages are random and membership redundant with little predictability as to why a given species is found in that location (Hubbell, 2001). Alternatively, deterministic processes could shape the success or failure of each fungal species at each site (Chesson, 2000; Chase and Leibold, 2003) with deterministic processes leading to assemblages that are predictable based on how species in the metacommunity interact with their environment and each other. As species differ in their ecological strategies (i.e., lifestyles; Table 1), deterministic processes favor some strategies establishing and succeeding in a given environment at a particular time over others. Species presence in a community is thought to be driven by both environmental filtering and biotic interactions winnowing out species unable to persist and compete under those conditions. Most likely, fungal communities fall somewhere on a spectrum between neutral and deterministic assembly (Chave, 2004), with parts of their assembly showing strong deterministic processes and a restricted region showing neutral or close to neutral dynamics (Powell et al., 2015).

The advent of high-throughput sequencing has rapidly sped up our ability to study fungal communities (Hibbett et al., 2009), and, as such, the search for a theoretical framework for fungal community ecology is at a nascent stage (Maherali and Klironomos, 2007; Bässler et al., 2014; van der Wal et al., 2016; Phillips et al., 2019). Aspects of theory emerging from other taxa may be useful in this effort. Plants, like fungi, are modular and sessile as adults, meaning theories developed in plants may transfer well to fungi, as suggested by Grime (1988) and Pugh (1980). In other taxa, ecological strategy schemes provide building blocks that shed light on mechanisms potentially allowing coexistence of diverse species assemblages.

An early scheme in plants was developed by Grime (1974) that suggested species could be arrayed along two axes in their environments: degree of stress and degree of disturbance. The expectation was that the axes could be divided into four boxes with species occupying three, described as: (1) competitors = low stress and low disturbance; (2) ruderals = low stress and high disturbance; and (3) stress tolerators = high stress and low disturbance with no species able to tolerate (4) high stress and high disturbance. There is no guidance in this scheme for how to measure a given species' location on these axes and compare these locations among different systems, as tolerating stress or being competitive are emergent properties. This shortcoming was tackled in subsequent schemes in which they directly mapped ecological strategies to the underlying mechanisms via species' functional traits - measurable properties i.e., morphological, anatomical, physiological, behavioral, etc. characteristic of a given species that inform when and where species are observed. We cover the rationale behind this focus below and go into the schemes in further depth in Table 1. In later sections, we highlight schemes we believe are especially ripe for development in understanding fungal community assembly.

The goal for the next generation of functional trait-based ecological strategy schemes (Reich et al., 1997, 1999) was to examine the tradeoffs and coordination (strategy axes) among traits that structure co-existence. Traits arise as a consequence of natural selection acting on the phenotype. As organisms must allocate their limited resources to optimize fitness, they cannot devote resources to all traits simultaneously (Bazzaz and Grace,

1997). This resource limitation results in coordination in some traits and tradeoffs in others (e.g., for a given mass of leaf tissues, leaves can maximize surface area to capture light or maximize thickness to withstand mechanical damage; Grime, 1979; Southwood, 1988; Craine, 2009). The trait spaces occupied by different species are constrained by species' available genetic variabilities, competitive abilities and biophysical possibilities (Reich et al., 1997; Preston et al., 2006). Because of the way these constraints interact with a changing environment in space and time, more than one successful strategy may exist within a particular environment, allowing the co-occurrence of functionally different organisms (Falster et al., 2017).

Some of the recognized critical functional traits in macro-organisms are measured at a micro-scale on a given organism (e.g., fine root diameter, vessel length and stomatal density), lending support for the idea of using traits to map fungal strategy schemes. Even so, functional trait data for fungi are only just beginning to emerge and the tool kit is largely limited to a subset of possible traits. Since many fungi are hard to observe, key traits to date focus on non-visual ones, including enzymatic and genetic. For instance, many wood decay fungi have numerous hydrolytic and lignolytic enzymes useful for breaking down complex carbon compounds (Eastwood et al., 2011; Riley et al., 2014). Other fungi lack various of these enzymes, especially lignolytic, which is strong evidence for an element of determinism in the assembly of wood decaying fungi. However, the dynamics among the species with hydrolytic and lignolytic enzymes may still show aspects of neutral behavior.

The potential for a trait-based ecology of fungi informed by individual strategy schemes developed for macro-organisms has been proposed in or inferred from multiple works (Table 1). This body of trait-based theory may be transferable to fungi, but it requires several major advances specific to fungi: (1) relevant traits need to be defined from careful study of fungal ecology, not just directly extrapolated from plants or other sessile modular organisms. Many of the existing schemes rely on measures of body size, which are difficult in fungi. Additionally, other key traits for macro-organisms do not occur in fungi (e.g., heterotrophic fungi have no direct analog to leaves in autotrophic plants but do have unique attributes to their fungal hyphae); (2) the distinct nature of fungal ecology e.g., bodies built of networks of hyphae has not been incorporated into strategy schemes for macro-organisms but is necessary for a theory of fungal community assemblies; (3) an approach to assembling and cataloguing the huge diversity of fungal communities needs to be developed. In this review, we discuss progress on all three fronts and describe a research program for moving forward in this final area.

2. Schemes overview

Many key strategy schemes used for various macro-organisms do not translate well to fungi (Table 1). Below we discuss ways that aspects of the most relevant may apply to, as well as unique challenges presented by, fungi as we strive to understand why so many fungal species exist on earth today. We divide our discussion of these schemes into four categories related to immigration: (1) dispersal and colonization and assembly; (2) growth rates and metabolism; (3) acquiring and deploying resources; as well as (4) lifestyle (guild) switching. The first three categories describe how a successful organism begins and lives out its life and the fourth describes a special ability of fungi to switch among lifestyles. As described above, strategies in these categories rest upon the idea that organisms are limited in their resources (Bazzaz and Grace, 1997), leading to tradeoffs in strategy and trait space. For instance, parents must choose how to allocate resources across

Table 1

Strategy schemes developed for various macro-organisms, including their description, potential problems applying them to fungi, original reference(s) and references in which they have been applied to fungi. Note: All schemes present serious problems when applying to fungi. Perhaps the most relevant is the competition-colonization strategy scheme, although only some aspects have yet to be tested in fungi. These issues suggest fungi-specific strategy schemes need to be developed.

Strategy Schemes	Description	Issues applying to fungi	Original reference	Fungal references
r - K	Represents tradeoff in reproductive strategies between producing many low investment offspring and few high investment offspring. Assumes parental investment.	Fungi can disperse without reproducing and parental investment does not translate.	(MacArthur and Wilson, 1967; Pianka, 1970)	(Andrews and Rouse, 1982; Andrews and Harris, 1986)
CSR	Allocates species into competitive, stress tolerators and ruderals.	No directly measurable traits meaning implementation is difficult within and across sites.	(Grime, 1974, 1979)	(Pugh, 1980; Pugh and Boddy, 1988; Chagnon et al., 2013; Boddy and Hiscox, 2016; Maynard et al., 2019)
Conservative - acquisitive	Places species along an axis of rates of return on investment with acquisitive species having high rates of acquisition and growth with conservative having the opposite.	Hyphal lifespan is difficult to measure. Specialized short-lifespan tissues are difficult to observe <i>in situ</i> or to measure <i>ex situ</i> .	Reich et al. (1999)	(Staddon et al., 2003; Powell and Rillig, 2018)
R*	Those with the ability to persist as resources become limiting (i.e., withstand indirect competition) will survive.	Direct competition is common in fungi, resource drawdown may be less important in determining outcomes. Fungi also often inhabit environments where resources are patchy.	Tilman (1982)	(Waldrop et al., 2006; Werner and Kiers, 2015)
Competition - colonization	Built on a tradeoff between ability to disperse to versus ability to establish at new sites.	Competitive hierarchies may not be simple.	Levins and Culver (1971)	(Hart et al., 2001; Kennedy et al., 2011)
Body size/metabolic scaling theory	Relates metabolic rates to body size with smaller bodied organisms thought to have higher mass-specific metabolic rates. Scaling slopes established for plants (1) and animals (3/4).	Body size in fungi is difficult both conceptually and practically.	Kleiber (1947)	Aguilar-Trigueros et al. (2017)
Stoichiometry	Predicts how the ratio of elements behave in organisms and substrates.	Plasticity in C:N:P on different substrates makes implementation tricky.	Sterner and Elser (2002)	(Johnson, 2010; Danger et al., 2016; Zhang and Elser, 2017; Powell and Rillig, 2018)
Allometric scaling	Predicts changes in organisms relative to proportional changes in body size.	Body size in fungi is difficult both conceptually and practically.	Corner (1949)	Aguilar-Trigueros et al. (2017)

offspring within and across years with consequences for their offsprings' abilities to colonize different sites. Additionally, as organisms grow, they also must choose how to allocate resources to different tissues and functions. These choices lead to variation in morphological and physiological allometries and nutrient distributions both in space and time, including shifting guild membership. Last, we discuss a major problem applying trait-based theories to fungi: the vast diversity of fungi has never been visually observed and are only known from sequencing; we propose a framework to facilitate data collection and overcome this hurdle.

3. Fungal strategy schemes

3.1. Dispersal and colonization

Assuming that organisms have finite resources to allocate to reproduction (Smith and Fretwell, 1974), offspring size should have a positive effect on individual survival and competitive ability and a negative effect on colonization if larger offspring have limited dispersal (Table 1: Competition-colonization and to a degree r-K). Across plants within habitats, a tradeoff between annual number and size of seeds produced has been observed (Moles and Westoby, 2006). On average, taller plants with smaller seeds disperse seeds further (Muller-Landau et al., 2008; Thomson et al., 2011), while seedlings of larger seeded species have higher survival through early establishment (Moles and Westoby, 2004) and are more tolerant of intra- (Lebrija-Trejos et al., 2016) and inter-specific neighbouring seedlings (Grime and Jeffrey, 1965; Walters and Reich, 2000) and established vegetation (Westoby et al., 2002). Based on these results from plants, a tradeoff is expected between spore number and size across fungal species. It is likely that this tradeoff will be maintained by biophysical constraints (e.g., space is limited in spore sacs, e.g., asci, basidia), as well as selective forces leading to common solutions across fungal taxa, weeding out less competitive strategies. Studies support some of these patterns in fungi. Spore size and number tradeoff (Chuang and Ko, 1983; Aguilar-Trigueros et al., 2019), and spore dispersal distance is negatively correlated with spore size (Norros et al., 2014). While, to our knowledge, direct evidence of the effect of spore size on the outcome of competitive interactions is lacking, modelling and experimental studies suggest that competitive ability is negatively linked to dispersal ability (Pringle and Taylor, 2002; Peay et al., 2007; Norros et al., 2014; Smith et al., 2018).

However, using spore size as a proxy for dispersal ability along the colonization-competition strategy axis may be inadequate. The adaptations that fungi possess for maximising dispersal are diverse in form and function (Ingold, 1954). Some fruiting bodies possess structures that serve to propel spores into the air, while spores possess a variety of traits that facilitate their movement via wind, plants, animals and water. In addition, fitness in novel environments appears to have more to do with spore dormancy and longevity than size (Nara, 2009). There may be more important traits than large spores enhancing viability in stressful environments, for instance attributes of fungal spore walls. For airborne spores, melanin may serve as protection against ultraviolet radiation over long distances (Jacobson et al., 1995), possibly at a cost of slower germination (Halbwachs and Bässler, 2015). Incorporating many of these diverse traits into a framework that places species along a fungal ecological strategy axis will be critical.

3.2. Growth and metabolism

Some existing strategies incorporate how organisms grow (Table 1; to a degree Stoichiometry, Conservative-acquisitive, CSR and Allometric scaling). Growth rate is not itself embedded in these

strategies, but rather is a measure of species performance in a particular environment given its ecological strategy. For instance, strategies associated with biological stoichiometry predict that fast growing plants tend to exhibit homeostatic tissue nitrogen:phosphorus (N:P) ratios that are constrained to a narrow range and less tightly linked to supply ratios of N and P in the environment, due to the coupled allocation of these elements into molecules supporting growth RNA molecules and proteins (Sterner and Elser, 2002; Elser et al., 2010). Work is needed to identify traits in fungi that provide a practical analog for some plant traits along this axis; for example, the N content in hyphae may confound attempts to map fungi on these axes given that it is also a component of structural chitin in addition to a component of molecules associated with growth.

Other elements of schemes focusing on growth may also be useful for fungi. For instance, the energy that fungi absorb can be transferred into metabolism or biomass, with the proportion that leads to biomass often quantified as "carbon use efficiency" (Sinsabaugh et al., 2013; Manzoni et al., 2018). Within biomass allocation, the energy can be allocated to hyphal growth or storage. Due largely to methodological limitations, carbon use efficiency has typically been measured at the community rather than species level. It is likely that there exists significant heterogeneity among fungal species in both their carbon use efficiency and allocation to growth versus storage, meaning that species level measures of carbon use efficiency for culturable, free-living fungi may prove a tractable trait. However, difficult to culture fungi and particularly those that are usually observed in association with a host will require conceptual and technological innovations. For instance, new approaches are needed to separate the amount of carbon assimilated and respired by a fungus from that associated with other organisms.

Metabolic rates (Table 1: Body size/metabolic scaling theory) have been frequently measured in plants and animals, where it is shown to scale with body size (West et al., 1997; Glazier, 2008). However, plants and animals typically follow different scaling relations between these variables (animals = 3/4 slope, plants = 1 slope), suggesting that metabolism, construction, and transport are governed by different laws between these two groups (Reich et al., 2006; Savage et al., 2008). In fungi, there have been few attempts to understand the scaling of biological functions with size; this is partly related to the fact that defining fungal body size is challenging (Aguilar-Trigueros et al., 2017). Often, we lack anything beyond a sequence for a given fungus, and even when we have fungal tissue in hand, it is hard to differentiate where a given individual begins and ends. One study used colony size to represent body size. They found when marine and ectomycorrhizal fungi were analyzed separately, metabolism scaled with colony size at approximately 0.58 (Aguilar-Trigueros et al., 2017), suggesting a lower metabolic rate for body size than recorded in animals and plants.

3.3. Acquiring and deploying resources

Once organisms establish at a site, they must acquire and deploy resources (Table 1: Stoichiometry and to a degree Conservative-acquisitive, R*, and Allometric scaling). There has been a strong historical focus on plant ecological strategies that drive resource acquisition (Wright et al., 2004; Ficken and Wright, 2019). However, directly extending this approach to fungi has been problematic because fungi, compared to plants, have very plastic growth characterized by less tissue differentiation; this flexibility allows them to shift along trait and ecological strategy axes in complex ways in response to shifting resources. Capturing key variation in growth strategies has led researchers to describe lists of applicable

Table 2
Measurable fungal traits. Adapted from Aguilar-Trigueros et al. (2015).

Trait category	Measurable traits
Mycelial architecture	Branching frequency, angle, order; Hyphal growth unit length; Internodal length; Lateral dichotomies; Rhizomorph/cord length and width; Runner hyphae length and width; Hyphal exploration type; Fractal dimension
Mycelial construction investment	Oxidases; Lignases; Cellulases; Phosphatases; Chitinases; Proteases; Iron transporters; Aquaporins; Chelators; Siderophores
Metabolism/enzymes	Nutrient concentrations; Stoichiometry (C:N:P); DNA, RNA, polyphosphate and lipid contents; Storage structures; Wall thickness; Hyphal diameter

fungal traits (Table 2), including mycelial architecture, construction investment, and enzyme expression. These traits underpin the diverse fungal nutrient acquisition strategies (Aguilar-Trigueros et al., 2015; Treseder and Lennon, 2015) that we link to ecological strategy schemes below. We believe these traits provide particularly useful avenues for future studies into fungal ecological strategies and community assembly.

Mycelial architecture, i.e., network structure, plays a significant role in resource acquisition (van der Heijden et al., 2006; Bebbler et al., 2007; Aguilar-Trigueros et al., 2015; Fricker et al., 2017) that is a flexible trait both within and among fungal species (Ritz and Crawford, 1990; Kranabetter et al., 2009; Olsson et al., 2014), potentially allowing co-occurring species to inhabit overlapping spaces but obtain different resources (Lehmann et al., 2018). This strategy axis may be key in explaining observable fungal diversity (Heijden and Scheublin, 2007; Koide et al., 2007). Mycelial architecture is linked to how resources flow through fungi. Fungi can change their network for optimal resource allocation by fusion among genetically similar hyphae to form supracellular networks (Weichert and Fleißner, 2015; Fleißner and Serrano, 2016). Loops created by these fusions provide physical pathways improving network resilience (Fricker et al., 2017). Additionally, mycelia have network recycling (Falconer et al., 2005; Heaton et al., 2016) in which regions “regress”, recycling contents. An open topic of research is predicting cues that direct fungi to strengthen or recycle particular fungal sections (Fricker et al., 2017).

Furthermore, fungi use different growth strategies to optimize resource uptake, including hyphae extending slowly and densely (short-range foragers or phalangeal foragers) versus extending rapidly but less-densely (long-range foragers) (Boddy, 1993, 1999; Agerer, 2001). The exploration type influences hyphal coverage per area of soil and functionality of single hyphae. Predictive models are being developed to understand network function. The key is that nutrient availability enables network growth and rapid growth is associated with rapid branching (Fricker et al., 2017). In these, network architecture is predicted from morphological characters, e.g., branching frequency and angle, internodal length, fractal dimension, and length and width of hyphal types (Lehmann et al., 2018), as well as the quantity and quality of the resources available (Boddy, 1999; Boddy et al., 2000; Fricker et al., 2017), and other biotic factors (Wood et al., 2006).

The mycelial construction investment is determined by hyphal structure and, together with external production of enzymes, plays an important role in spatial foraging strategies of fungi. Morphological characters of thin hyphae allow fungi to penetrate deep into substrates and grow through solid material to obtain nutrients (van der Wal et al., 2015). The mycelial construction investment strategy axis includes morphological traits such as wall thickness, hyphal diameter and stoichiometry (Sinsabaugh et al., 2008; Aguilar-Trigueros et al., 2015). The nutrient content, or stoichiometry, differs among fungal species (Mouginot et al., 2014; Tischer et al., 2014) and guilds (Zhang and Elser, 2017; Kranabetter et al., 2019). In all organisms, growth is greatest when neither N nor P are limiting and both are allocated to compounds required for growth

(Elser et al., 2003). During growth, N is allocated to structural compounds (e.g., chitin) and proteins and P is allocated to nucleic acids and membrane phospholipids (Bull and Trinci, 1977). When nutrient availability exceeds growth requirements, N and P concentrations in vacuoles increase (Kottke et al., 1995). In addition to playing a role in translocation of P to the plant host in mutualistic symbiotic fungi (Bücking and Heyser, 1999; Ezawa et al., 2004), polyphosphates are associated with conditions of slow growth and stress and their contribution to the total P pool varies among fungal species on the order of 23–65% (Beever and Burns, 1981).

Finally, resource acquisition depends on enzyme expression, which functions to increase nutrient availability for uptake (Allison and Vitousek, 2005; Aguilar-Trigueros et al., 2015; Treseder and Lennon, 2015). Because fungi are heterotrophs, they must extract energy from other organisms – living and dead. To do this, most secrete extracellular enzymes to break down compounds obtaining monomers as carbon. Fungi are typically divided into three major nutrient acquisition functional groups: mutualistic, parasitic and saprotrophic (Murphy and Horgan, 2005; Nguyen et al., 2016; Zeilinger et al., 2016). Although these groups differ in the set and expression level of enzymes, genomic studies are showing that a continuous trait-based approach is needed to determine fungal functionality (Peay et al., 2016). For example, while mutualistic mycorrhizal and parasitic fungi obtain their carbon via their hosts, saprotrophs gain their carbon from dead organic materials, such as soil and litter. However, ectomycorrhizal fungi cannot be clearly distinguished from their free-living saprotroph relatives based on enzyme expression alone (Talbot et al., 2015). Like their relatives, they can decompose litter and only have lower expression of carbohydrases, acid phosphatases (Talbot et al., 2015) and peroxidases (Kyaschenko et al., 2017) than their relatives (Rineau et al., 2012; Lindahl and Tunlid, 2015; Shah et al., 2016). Because enzyme expression levels differ dramatically among species, understanding this resource strategy axis is key to understanding fungal functionality, abundance and survival (Snajdr et al., 2011; Eichlerová et al., 2015). Depending on the community of fungi, different enzymes are secreted and niches occupied, which has strong ecological effects (van der Wal et al., 2015; Baskaran et al., 2017). This axis is likewise an important driver for fungal diversity by driving niche differentiation (Caldwell, 2005; Heijden and Scheublin, 2007). To sum up, while fungi may acquire resources in different ways to those described already for macro-organisms, a growing body of literature suggests promise in critical fungal traits in resource acquisition and deployment, which should allow for fungal specific strategy schemes.

3.4. Lifestyle (guild) switching

Fungi present a unique challenge as we attempt to translate ecological strategy schemes from macro-organisms; they traverse ecological guilds and trophic levels (Olson et al., 2012; Voříšková and Baldrian, 2013; Kuo et al., 2014; Martin et al., 2015; Zanne et al., in press). They are pathogens of animals and plants, causing disease and death in hosts, endophytes existing within host tissues,

mutualistic symbionts such as lichens and mycorrhizas exchanging resources with hosts, and saprotrophs decomposing dead organic material (<https://github.com/UMNFuN/FUNGuild>). Some fungi even exist as parasites on other fungi (i.e., mycoparasites; Barnett, 1963). Many fungi can move among being pathogens, mutualists and saprobes over the course of a given individual's life or among individuals of the same species (Olson et al., 2012; Voříšková and Baldrian, 2013; Kuo et al., 2014; Martin et al., 2015; Zanne et al., in press). It may be that the ecological strategies and the traits that underpin those strategies change with a change in guild, requiring different schemes applied within and across species.

Plants also show a range of guilds from carnivore to parasite to epiphyte, but this range has largely been ignored by both trait ecology and coexistence models, under the assumption that most "important" plants share the same, free-standing, autotrophic strategy. This type of assumption is less defensible in fungi, as there are more species that switch guilds, and it is expected that switching offers a competitive advantage. For example, saprotrophs often already occupy wood as endophytes and have a distinct edge in competing for resources as compared to species that need to disperse to the substrate (Parfitt et al., 2010). Similarly, the dynamics of switching between mutualist and saprobe is an important part of the ecology of many mycorrhizal fungi (Talbot et al., 2008; but see Lindahl and Tunlid, 2015). As strategy schemes are developed for fungi, they must incorporate the incredible ability of fungi to readily move among guilds as it is clearly the rule, not the exception.

3.4.1. Research program: towards an understanding of fungal traits and strategy schemes across gradients

Our review of existing ecological strategy axes developed for macro-organisms suggests that many of them will not be readily recycled to fungi. For instance, many rely upon visual observations of organisms, especially measures of body size, which are not feasible for many fungi. These findings suggest that while elements of existing schemes may be useful, new ones must be developed. Empirical data were key to the development of functional strategy schemes for various macro-organisms. For example, shifts in plant trait distributions across different soil types and grazing pressures near Sheffield were two of a number of key empirical observations that lead to the CSR scheme (Grime, 1974). One critical empirical limitation in the development of fungal strategy schemes is the lack of data to make analogous observations.

Fungal diversity at all scales is daunting. Even more troublesome is that, unlike for various macro-organisms, it is often impossible to isolate an individual species to measure traits. This challenge creates a difficult problem for fungal ecologists: they can use high-throughput sequencing to measure amplicon or shotgun sequences for operational taxonomic units ("species") in a community, but are able to isolate only a small subset of these organisms for further study. The traits and strategies of the unisolated species remain a mystery. This limitation prevents key observations such as those that lead to CSR and other strategy schemes.

Central to this process is the need to fill gaps in the available trait data (Zanne et al., in press), particularly with fungal species that are difficult to culture or are only found in association with hosts. Linking high-throughput sequences to traits and strategies will open an array of research opportunities in fungal ecology and evolutionary biology, leading to a new golden age for fungal function. For an example of how this might be done, we consider growth, which relates to many ecological strategy schemes (Table 1) but is challenging to measure for species of fungi that cannot be observed *in vitro* since it is difficult to assess their biomass or surface area. Combining measures of these traits on environmental samples with DNA-based tools to identify species

may be an indirect way to characterise their growth. Investigations into fungal growth going back to Tomkins (1932), focusing on hyphal extension and branching, suggest ways to extrapolate to growth from a portion of a mycelium. The frequency of hyphal tip production can be inferred from the length between branches (Trinci, 1974). Steele and Trinci (1975) observed that hyphal extension was strongly correlated with the length of the extension zone, from the tip of the extending hypha where hyphal diameter is expanding to its base where the wall has matured and hyphal diameter is fixed. These measures can be made so that samples are left intact to then use DNA sequencing to identify species present.

Furthermore, much may be gleaned from the combined use of trait data measured on species and high-throughput amplicon or shotgun sequencing of environmental samples, to map the distribution of fungal species and their traits across environments, and infer the deterministic drivers of fungal community assembly. However, for many traits, the tools and resources are not yet available. Below we outline the steps necessary for this to occur:

1. Measuring more species for a narrow set of traits (Aguilar-Trigueros et al., 2015) in standard conditions. In plants, growth experiments have assembled large databases of relative growth rates, in a process originally called "trait screening" (Grime et al., 1997; Poorter et al., 2019). The process of assembling fungal data has begun (Aguilar-Trigueros et al., 2015; Treseder and Lennon, 2015; Dawson et al., 2019; Zanne et al., in press; <https://github.com/traitecoevo/fungaltraits>), but we need to assemble larger, more-comprehensive, global databases starting with an agreed upon set of traits relevant to important ecological strategies (e.g., Table 2).
2. Linking trait measures to sequence data collected from voucher specimens and other sampled fungi via repeatable pipelines using taxonomic names and/or accession numbers. These links will allow us to apply trait values to species we find in different communities.
3. Building a comprehensive phylogeny of fungi populated by taxa with trait values.
4. Modelling evolution of traits on the phylogeny, including understanding the tempo and mode, *sensu* Simpson (1944), of trait evolution (e.g., test for adequacy of different evolutionary models). Building a phylogeny and modelling trait evolution will let us determine the importance of evolutionary history in shaping community assembly and understand how different traits evolved across the fungal tree of life.
5. Using modern mapping and grafting methods to add novel amplicon sequences lacking trait values to the phylogeny (Beaulieu et al., 2012; Smith et al., 2013; Smith and Brown, 2018). As we have only uncovered a small slice of fungal diversity, it will be critical to grow our evolutionary tree as we discover more of this hidden diversity.
6. Imputing trait values for the amplicon sequences along with associated uncertainty (due to phylogenetic, trait, and imputation uncertainty). Methods for this already exist (FitzJohn et al., 2014; Penone et al., 2014; Swenson, 2014; Schrodt et al., 2015) and the choice of specific methods will be informed by the results of (4). As taxa missing trait values are added to the phylogeny, we can predict what trait and ecological strategy space they may occupy. These estimates may in some cases be directly used in analyses of communities and in others provide testable hypotheses as we are able to collect trait data directly for those species.

These steps have been useful in shaping our understanding of, for instance, plant functional ecology, evolution and community assembly. They should similarly facilitate rapid growth in our

understanding of fungi and be attainable in the next 10 y of fungal research. As linked databases and tools are created, novel answers to outstanding questions will be found, as well as insight into a new generation of strategy schemes specific for fungi. We believe we can open the door to previously unanswerable questions about fungal functional ecology including: How redundant are fungal communities? Does the growth rate of fungi slow as succession proceeds in forests? Do fungi in patchier soils show different hyphal branching networks than homogeneous soils? Is fungal community assembly dominated by habitat filtering or is there also a role for limiting similarity? Is the average growth rate of tropical fungi faster than temperate fungi? Do urban fungi have different traits than those from natural habitats? Are climate change and intensification of land use exerting selection on traits associated with growth and resource allocation? Do the traits of mycorrhizal symbionts change as a tree matures? Are fungi able to change ecological strategies and traits as they shift their nutritional modes, as their host substrate changes, and/or as they interact with other fungi in their community? These questions are interesting in their own right, but also the answers will provide the key empirical data to develop fungi-specific strategy schemes.

4. Conclusion

We propose that recycling ecological strategy schemes developed for macro-organisms is a worthwhile starting point for developing a functional understanding of fungal diversity; however, translating many of these existing schemes will prove challenging. We have provided an overview of hurdles associated with fungi that need to be overcome, including elements of their biology and life histories that are special and suggest that existing ecological strategies may need to be rethought or revised. For instance, many existing ecological strategy schemes rely on measures of body size, which is often difficult to define for fungi. Particularly challenging is filling the massive gap in data required to map the diversity of fungi to ecological strategy schemes, but the research program we have proposed has tremendous potential to make a substantial contribution toward this effort. Realizing this potential will require the combined efforts of mycologists and those from many other disciplines (physiology, molecular biology, ecological informatics, phylogenomics, etc.).

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References

Adams, R.I., Miletto, M., Taylor, J.W., Bruns, T.D., 2013. Dispersal in microbes: fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances. *ISME J.* 7, 1262–1273. <https://doi.org/10.1038/ismej.2013.28>.
 Agerer, R., 2001. Exploration types of ectomycorrhizae. *Mycorrhiza* 11, 107–114. <https://doi.org/10.1007/s005720100108>.
 Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J., Cavagnaro, T.R., Chen, B., Hart, M.M., Klironomos, J., Petermann, J.S., Verbruggen, E., Veresoglou, S.D., Rillig, M.C., 2015. Branching out: towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews* 29, 34–41. <https://doi.org/10.1016/j.fbr.2015.03.001>.

Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Cornwell, W.K., Rillig, M.C., 2019. Bridging reproductive and microbial ecology: a case study in arbuscular mycorrhizal fungi. *ISME J.* 13, 873. <https://doi.org/10.1038/s41396-018-0314-7>.
 Aguilar-Trigueros, C.A., Rillig, M.C., Crowther, T.W., 2017. Applying allometric theory to fungi. *ISME J.* 11, 2175–2180. <https://doi.org/10.1038/ismej.2017.86>.
 Allison, S.D., Vitousek, P.M., 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biol. Biochem.* 37, 937–944. <https://doi.org/10.1016/j.soilbio.2004.09.014>.
 Andrews, J.H., Harris, R.F., 1986. R- and K-selection and microbial ecology. In: Marshall, K.C. (Ed.), *Advances in Microbial Ecology*, Advances in Microbial Ecology, vol 9. Springer US, Boston, MA, pp. 99–147. https://doi.org/10.1007/978-1-4757-0611-6_3.
 Andrews, J.H., Rouse, D.I., 1982. Plant pathogens and the theory of r- and K-selection. *Am. Nat.* 120, 283–296.
 Barnett, H.L., 1963. The nature of mycoparasitism by fungi. *Annu. Rev. Microbiol.* 17, 1–14. <https://doi.org/10.1146/annurev.mi.17.100163.000245>.
 Bar-On, Y.M., Phillips, R., Milo, R., 2018. The biomass distribution on Earth. *Proc. Natl. Acad. Sci.* 115, 6506–6511. <https://doi.org/10.1073/pnas.1711842115>.
 Baskaran, P., Hyvönen, R., Berglund, S.L., Clemmensen, K.E., Ågren, G.I., Lindahl, B.D., Manzoni, S., 2017. Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. *New Phytol.* 213, 1452–1465. <https://doi.org/10.1111/nph.14213>.
 Bässler, C., Ernst, R., Cadotte, M., Heibl, C., Müller, J., 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. *J. Appl. Ecol.* 51, 939–948.
 Bazzaz, F., Grace, J. (Eds.), 1997. *Plant Resource Allocation*. Elsevier. <https://doi.org/10.1016/B978-0-12-083490-7.X5000-2>.
 Beaulieu, J.M., Ree, R.H., Cavender-Bares, J., Weiblen, G.D., Donoghue, M.J., 2012. Synthesizing phylogenetic knowledge for ecological research. *Ecology* 93, S4–S13. <https://doi.org/10.1890/11-0638.1>.
 Bebbler, D.P., Hynes, J., Darrah, P.R., Boddy, L., Fricker, M.D., 2007. Biological solutions to transport network design. *Proc. R. Soc. Biol. Sci.* 274, 2307–2315. <https://doi.org/10.1098/rspb.2007.0459>.
 Beaver, R.E., Burns, D.J.W., 1981. Phosphorus uptake, storage and utilization by fungi. In: Woolhouse, H.W. (Ed.), *Advances in Botanical Research*. Academic Press, pp. 127–219. [https://doi.org/10.1016/S0065-2296\(08\)60034-8](https://doi.org/10.1016/S0065-2296(08)60034-8).
 Boddy, L., 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia* 91, 13–32. <https://doi.org/10.2307/3761190>.
 Boddy, L., 1993. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycol. Res.* 97, 641–655. [https://doi.org/10.1016/S0953-7562\(09\)80141-X](https://doi.org/10.1016/S0953-7562(09)80141-X).
 Boddy, L., Hiscox, J., 2016. Fungal ecology: principles and mechanisms of colonization and competition by saprotrophic fungi. *Microbiol. Spectr.* 4. <https://doi.org/10.1128/microbiolspec.FUNK-0019-2016>.
 Boddy, L., Wells, J.M., Culshaw, C., Donnelly, D.P., 2000. Fractal analysis in studies of mycelium in soil. In: Pachepey, Y., Crawford, J.W., Rawls, W.J. (Eds.), *Developments in Soil Science*, Fractals in Soil Science. Elsevier, pp. 211–238. [https://doi.org/10.1016/S0166-2481\(00\)80014-8](https://doi.org/10.1016/S0166-2481(00)80014-8).
 Bücking, H., Heyser, W., 1999. Elemental composition and function of polyphosphates in ectomycorrhizal fungi – an X-ray microanalytical study. *Mycol. Res.* 103, 31–39. <https://doi.org/10.1017/S0953756298006935>.
 Bull, A.T., Trinci, A.P.J., 1977. The physiology and metabolic control of fungal growth. In: Rose, A.H., Tempest, D.W. (Eds.), *Advances in Microbial Physiology*. Academic Press, pp. 1–84. [https://doi.org/10.1016/S0065-2911\(08\)60314-8](https://doi.org/10.1016/S0065-2911(08)60314-8).
 Caldwell, B.A., 2005. Enzyme activities as a component of soil biodiversity: a review. *Pedobiologia* 49, 637–644. <https://doi.org/10.1016/j.pedobi.2005.06.003>.
 Chagnon, P.-L., Bradley, R.L., Maherali, H., Klironomos, J.N., 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends Plant Sci.* 18, 484–491. <https://doi.org/10.1016/j.tplants.2013.05.001>.
 Chase, J., Leibold, M., 2003. *Ecological Niches*. The University of Chicago Press, Chicago, IL, USA.
 Chase, J., 2004. Neutral theory and community ecology. *Ecol. Lett.* 7, 241–253. <https://doi.org/10.1111/j.1461-0248.2003.00566.x>.
 Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Systemat.* 31, 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>.
 Chuang, T.Y., Ko, W.H., 1983. Propagule size: its relation to longevity and reproductive capacity. *Soil Biol. Biochem.* 15, 269–274. [https://doi.org/10.1016/0038-0717\(83\)90070-6](https://doi.org/10.1016/0038-0717(83)90070-6).
 Corner, E.J.H., 1949. The durian theory or the origin of the modern tree. *Ann. Bot.* 13, 367–414.
 Craine, J.M., 2009. *Resource Strategies of Wild Plants*. Princeton University Press.
 Danger, M., Gessner, M.O., Bärlocher, F., 2016. Ecological stoichiometry of aquatic fungi: current knowledge and perspectives. *Fungal Ecology, Aquatic Fungi* 19, 100–111. <https://doi.org/10.1016/j.funeco.2015.09.004>.
 Dawson, S.K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., Heilmann-Clausen, J., Nordén, J., Ovaskainen, O., Jönsson, M., 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. *Funct. Ecol.* 33, 372–387. <https://doi.org/10.1111/1365-2435.13239>.
 Eastwood, D.C., Floudas, D., Binder, M., Majcherzyk, A., Schneider, P., Aerts, A., Asiegbu, F.O., Baker, S.E., Barry, K., Bendiksby, M., Blumentritt, M., Coutinho, P.M., Cullen, D., Vries, R.P. de, Gathman, A., Goodell, B., Henriessat, B., Ihrmark, K., Kauterud, H., Kohler, A., LaButti, K., Lapidus, A., Lavin, J.L., Lee, Y.-H., Lindquist, E., Lilly, W., Lucas, S., Morin, E., Murat, C., Oguiza, J.A., Park, J.,

- Pisabarro, A.G., Riley, R., Rosling, A., Salamov, A., Schmidt, O., Schmutz, J., Skrede, I., Stenlid, J., Wiebenga, A., Xie, X., Kües, U., Hibbett, D.S., Hoffmeister, D., Högberg, N., Martin, F., Grigoriev, I.V., Watkinson, S.C., 2011. The plant cell wall—decomposing machinery underlies the functional diversity of forest fungi. *Science* 333, 762–765. <https://doi.org/10.1126/science.1205411>.
- Egidi, E., Delgado-Baquerizo, M., Plett, J.M., Wang, J., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., 2019. A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat. Commun.* 10, 2369. <https://doi.org/10.1038/s41467-019-10373-z>.
- Eichlerová, I., Homolka, L., Žifčáková, L., Lisá, L., Dobiášová, P., Baldrian, P., 2015. Enzymatic systems involved in decomposition reflects the ecology and taxonomy of saprotrophic fungi. *Fungal Ecology* 13, 10–22. <https://doi.org/10.1016/j.funeco.2014.08.002>.
- Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., Watts, T., Hobbie, S., Fagan, W., Schade, J., Hood, J., Sterner, R.W., 2003. Growth rate—stoichiometry couplings in diverse biota. *Ecol. Lett.* 6, 936–943. <https://doi.org/10.1046/j.1461-0248.2003.00518.x>.
- Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G., Enquist, B.J., 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytol.* 186, 593–608.
- Ezawa, T., Cavnagaro, T.R., Smith, S.E., Smith, F.A., Ohtomo, R., 2004. Rapid accumulation of polyphosphate in extracellular hyphae of an arbuscular mycorrhizal fungus as revealed by histochemistry and a polyphosphate kinase/luciferase system. *New Phytol.* 161, 387–392. <https://doi.org/10.1046/j.1469-8137.2003.00966.x>.
- Falconer, R.E., Bown, J.L., White, N.A., Crawford, J.W., 2005. Biomass recycling and the origin of phenotype in fungal mycelia. *Proc. Biol. Sci.* 272, 1727–1734. <https://doi.org/10.1098/rspb.2005.3150>.
- Falster, D.S., Brännström, Å., Westoby, M., Dieckmann, U., 2017. Multitrait successional forest dynamics enable diverse competitive coexistence. *Proc. Natl. Acad. Sci.* 114, E2719–E2728. <https://doi.org/10.1073/pnas.1610206114>.
- Ficken, C.D., Wright, J.P., 2019. Nitrogen uptake and biomass resprouting show contrasting relationships with resource acquisitive and conservative plant traits. *J. Veg. Sci.* 30, 65–74. <https://doi.org/10.1111/jvs.12705>.
- FitzJohn, R.G., Pennell, M.W., Zanne, A.E., Stevens, P.F., Tank, D.C., Cornwell, W.K., 2014. How much of the world is woody? *J. Ecol.* 102, 1266–1272. <https://doi.org/10.1111/1365-2745.12260>.
- Fleißner, A., Serrano, A., 2016. 7 the art of networking: vegetative hyphal fusion in filamentous ascomycete fungi. In: Wendland, J. (Ed.), *Growth, Differentiation and Sexuality, the Mycota*. Springer International Publishing, Cham, pp. 133–153. https://doi.org/10.1007/978-3-319-25844-7_7.
- Fricker, M.D., Heaton, L.L.M., Jones, N.S., Boddy, L., 2017. The mycelium as a network. *Microbiol. Spectr.* 5 <https://doi.org/10.1128/microbiolspec.FUNK-0033-2017>.
- Glazier, D.S., 2008. Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals. *Proc. Biol. Sci.* 275, 1405–1410. <https://doi.org/10.1098/rspb.2008.0118>.
- Green, J.L., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M., Beattie, A.J., 2004. Spatial scaling of microbial eukaryote diversity. *Nature* 432, 747–750. <https://doi.org/10.1038/nature03034>.
- Grime, J.P., 1988. Fungal strategies in ecological perspective. *Proc. Roy. Soc. Edinb. Sect. B Biol. Sci.* 94, 167–169. <https://doi.org/10.1017/S0269727000007260>.
- Grime, J.P., 1974. *Vegetation classification by reference to strategies*. *Nature* 250, 26–31.
- Grime, J.P., Jeffrey, D.W., 1965. Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53, 621–642. <https://doi.org/10.2307/2257624>.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C., Whitehouse, J., 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79, 259–281. <https://doi.org/10.2307/3546011>.
- Grime, P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK.
- Halbwachs, H., Bässler, C., 2015. Gone with the wind - a review on basidiospores of lamellate agarics. *Mycosphere* 6. <https://doi.org/10.5943/mycosphere/6/1/10>.
- Hart, M.M., Reader, R.J., Klironomos, J.N., 2001. Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. *Mycologia* 93, 1186–1194. <https://doi.org/10.2307/3761678>.
- Hawksworth, D.L., Lücking, R., 2017. Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiol. Spectr.* 5 <https://doi.org/10.1128/microbiolspec.FUNK-0052-2016>.
- Heaton, L.L.M., Jones, N.S., Fricker, M.D., 2016. Energetic constraints on fungal growth. *Am. Nat.* 187, E27–E40. <https://doi.org/10.1086/684392>.
- Heijden, M.G.A.V.D., Scheublin, T.R., 2007. Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytol.* 174, 244–250. <https://doi.org/10.1111/j.1469-8137.2007.02041.x>.
- Hibbett, D.S., Ohman, A., Kirk, P.M., 2009. Fungal ecology catches fire. *New Phytol.* 184, 279–282. <https://doi.org/10.1111/j.1469-8137.2009.03042.x>.
- Hu, Y., Veresoglou, S.D., Tedersoo, L., Xu, T., Ge, T., Liu, L., Chen, Y., Hao, Z., Su, Y., Rillig, M.C., Chen, B., 2019. Contrasting latitudinal diversity and co-occurrence patterns of soil fungi and plants in forest ecosystems. *Soil Biol. Biochem.* 131, 100–110. <https://doi.org/10.1016/j.soilbio.2019.01.001>.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography* (MPB-32). Princeton University Press.
- Ingold, C., 1954. *Dispersal in Fungi*. Clarendon Press, Oxford.
- Jacobson, E.S., Hove, E., Emery, H.S., 1995. Antioxidant function of melanin in black fungi. *Infect. Immun.* 63, 4944–4945.
- Johnson, N.C., 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytol.* 185, 631–647. <https://doi.org/10.1111/j.1469-8137.2009.03110.x>.
- Kemmel, S.W., Mueller, R.C., 2014. Plant traits and taxonomy drive host associations in tropical phyllosphere fungal communities. *Botany* 92, 303–311. <https://doi.org/10.1139/cjb-2013-0194>.
- Kennedy, P.G., Higgins, L.M., Rogers, R.H., Weber, M.G., 2011. Colonization-competition tradeoffs as a mechanism driving successional dynamics in ectomycorrhizal fungal communities. *PLoS One* 6, e25126. <https://doi.org/10.1371/journal.pone.0025126>.
- Kleiber, M., 1947. Body size and metabolic rate. *Physiol. Rev.* 27, 511–541. <https://doi.org/10.1152/physrev.1947.27.4.511>.
- Koide, R.T., Courty, P.-E., Garbaye, J., 2007. Research perspectives on functional diversity in ectomycorrhizal fungi. *New Phytol.* 174, 240–243. <https://doi.org/10.1111/j.1469-8137.2007.01987.x>.
- Kottke, I., Holopainen, T., Alanen, E., Turnau, K., 1995. Deposition of nitrogen in vacuolar bodies of *Cenococcum geophilum* Fr. mycorrhizas as detected by electron energy loss spectroscopy. *New Phytol.* 129, 411–416. <https://doi.org/10.1111/j.1469-8137.1995.tb04311.x>.
- Kranabetter, J.M., Durall, D.M., MacKenzie, W.H., 2009. Diversity and species distribution of ectomycorrhizal fungi along productivity gradients of a southern boreal forest. *Mycorrhiza* 19, 99–111. <https://doi.org/10.1007/s00572-008-0208-z>.
- Kranabetter, J.M., Harman-Denhoed, R., Hawkins, B.J., 2019. Saprotrophic and ectomycorrhizal fungal sporocarp stoichiometry (C : N : P) across temperate rainforests as evidence of shared nutrient constraints among symbionts. *New Phytol.* 221, 482–492. <https://doi.org/10.1111/nph.15380>.
- Kuo, H.-C., Hui, S., Choi, J., Asiegbu, F.O., Valkonen, J.P.T., Lee, Y.-H., 2014. Secret lifestyles of *Neurospora crassa*. *Sci. Rep.* 4, srep05135. <https://doi.org/10.1038/srep05135>.
- Kyaschenko, J., Clemmensen, K., Karlton, E., Lindahl, B., 2017. Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecol. Lett.* 20, 1546–1555.
- Larsen, B.B., Miller, E.C., Rhodes, M.K., Wiens, J.J., 2017. Inordinate fondness multiplied and redistributed: the number of species on earth and the new pie of life. *Q. Rev. Biol.* 92, 229–265. <https://doi.org/10.1086/693564>.
- Lebrija-Trejos, E., Reich, P.B., Hernández, A., Wright, S.J., 2016. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecol. Lett.* 19, 1071–1080. <https://doi.org/10.1111/ele.12643>.
- Lee, M.R., Powell, J.R., Oberle, B., Cornwell, W.K., Lyons, M., Rigg, J.L., Zanne, A.E., 2019. Good neighbors aplenty: fungal endophytes rarely exhibit competitive exclusion patterns across a span of woody habitats. *Ecology* 100, e02790. <https://doi.org/10.1002/ecy.2790>.
- Lehmann, A., Zheng, W., Soutschek, K., Rillig, M., 2018. How to build a mycelium: tradeoffs in fungal architectural traits. *bioRxiv*. <https://doi.org/10.1101/361253>.
- Levins, R., Culver, D., 1971. Regional coexistence of species and competition between rare species. *Proc. Natl. Acad. Sci. U.S.A.* 68, 1246–1248. <https://doi.org/10.1073/pnas.68.6.1246>.
- Lindahl, B.D., Tunlid, A., 2015. Ectomycorrhizal fungi - potential organic matter decomposers, yet not saprotrophs. *New Phytol.* 205, 1443–1447. <https://doi.org/10.1111/nph.13201>.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press.
- Maherali, H., Klironomos, J.N., 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316, 1746–1748. <https://doi.org/10.1126/science.1143082>.
- Manzoni, S., Capek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Brüchert, V., Frouz, J., Herrmann, A.M., Lindahl, B.D., Lyon, S.W., Šantrůčková, H., Vico, G., Way, D., 2018. Reviews and syntheses: carbon use efficiency from organisms to ecosystems – definitions, theories, and empirical evidence. *Biogeosciences* 15, 5929–5949. <https://doi.org/10.5194/bg-15-5929-2018>.
- Martin, R., Gazis, R., Skaltsas, D., Chaverri, P., Hibbett, D., 2015. Unexpected diversity of basidiomycetous endophytes in sapwood and leaves of *Hevea*. *Mycologia* 107, 284–297. <https://doi.org/10.3852/14-206>.
- Maynard, D.S., Bradford, M.A., Covey, K.R., Lindner, D., Glaeser, J., Talbert, D.A., Tinker, P.J., Walker, D.M., Crowther, T.W., 2019. Consistent trade-offs in fungal trait expression across broad spatial scales. *Nature Microbiology* 4, 846. <https://doi.org/10.1038/s41564-019-0361-5>.
- Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92, 372–383.
- Moles, A.T., Westoby, M., 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113, 91–105. <https://doi.org/10.1111/j.0030-1299.2006.14194.x>.
- Mouginot, C., Kawamura, R., Matulich, K.L., Berlemont, R., Allison, S.D., Amend, A.S., Martiny, A.C., 2014. Elemental stoichiometry of Fungi and Bacteria strains from grassland leaf litter. *Soil Biol. Biochem.* 76, 278–285. <https://doi.org/10.1016/j.soilbio.2014.05.011>.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R., Hubbell, S.P., 2008. Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* 96, 653–667. <https://doi.org/10.1111/j.1365-2745.2008.01399.x>.
- Murphy, R.A., Horgan, K.A., 2005. Antibiotics, enzymes and chemical commodities

- from fungi. In: *Fungi*. John Wiley & Sons, Ltd, pp. 113–143. <https://doi.org/10.1002/0470015330.ch5>.
- Nara, K., 2009. Spores of ectomycorrhizal fungi: ecological strategies for germination and dormancy. *New Phytol.* 181, 245–248. <https://doi.org/10.1111/j.1469-8137.2008.02691.x>.
- Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* 20, 241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>.
- Norros, V., Rannik, U., Hussein, T., Petäjä, T., Vesala, T., Ovaskainen, O., 2014. Do small spores disperse further than large spores? *Ecology* 95, 1612–1621.
- Olson, A., Aerts, A., Asiegbu, F., Belbahri, L., Bouzid, O., Broberg, A., Canbäck, B., Coutinho, P.M., Cullen, D., Dalman, K., DeFlorio, G., van Diepen, L.T.A., Dunand, C., Duplessis, S., Durling, M., Gonthier, P., Grimwood, J., Fossdal, C.G., Hansson, D., Henrissat, B., Hietala, A., Himmelstrand, K., Hoffmeister, D., Högberg, N., James, T.Y., Karlsson, M., Kohler, A., Kues, U., Lee, Y.-H., Lin, Y.-C., Lind, M., Lindquist, E., Lombard, V., Lucas, S., Lundén, K., Morin, E., Murat, C., Park, J., Raffaello, T., Rouzé, P., Salamov, A., Schmutz, J., Solheim, H., Stahlberg, J., Vélez, H., de Vries, R.P., Wiebenga, A., Woodward, S., Yakovlev, I., Garbelotto, M., Martin, F., Grigoriev, I.V., Stenlid, J., 2012. Insight into trade-off between wood decay and parasitism from the genome of a fungal forest pathogen. *New Phytol.* 194, 1001–1013. <https://doi.org/10.1111/j.1469-8137.2012.04128.x>.
- Olsson, O., Olsson, P.A., Hammer, E.C., 2014. Phosphorus and carbon availability regulate structural composition and complexity of AM fungal mycelium. *Mycorrhiza* 24, 443–451. <https://doi.org/10.1007/s00572-014-0557-8>.
- Parfitt, D., Hunt, J., Dockrell, D., Rogers, H.J., Boddy, L., 2010. Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecology* 3, 338–346. <https://doi.org/10.1016/j.funeco.2010.02.001>.
- Peay, K., 2007. Are all fungi everywhere? [WWW Document] MykoWeb: Mushrooms, Fungi, Mycology. <http://www.mykoweb.com/articles/Are-All-Fungi-Everywhere.html>, 7.18.2019.
- Peay, K.G., Bidartondo, M.I., Arnold, A.E., 2010. Not every fungus is everywhere: scaling to the biogeography of fungal–plant interactions across roots, shoots and ecosystems. *New Phytol.* 185, 878–882. <https://doi.org/10.1111/j.1469-8137.2009.03158.x>.
- Peay, K.G., Bruns, T.D., Kennedy, P.G., Bergemann, S.E., Garbelotto, M., 2007. A strong species-area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecol. Lett.* 10, 470–480. <https://doi.org/10.1111/j.1461-0248.2007.01035.x>.
- Peay, K.G., Kennedy, P.G., Talbot, J.M., 2016. Dimensions of biodiversity in the Earth microbiome. *Nat. Rev. Microbiol.* 14, 434–447. <https://doi.org/10.1038/nrmicro.2016.59>.
- Penone, C., Davidson, A.D., Shoemaker, K.T., Marco, M.D., Rondinini, C., Brooks, T.M., Young, B.E., Graham, C.H., Costa, G.C., 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 5, 961–970. <https://doi.org/10.1111/2041-210X.12232>.
- Phillips, M.L., Weber, S.E., Andrews, L.V., Aronson, E.L., Allen, M.F., Allen, E.B., 2019. Fungal community assembly in soils and roots under plant invasion and nitrogen deposition. *Fungal Ecology* 40, 107–117.
- Pianka, E.R., 1970. On r - and K -Selection. *Am. Nat.* 104, 592–597.
- Poorter, H., Niinemets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S., Pons, T., 2019. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytol.* 223, 1073–1105. <https://doi.org/10.1111/nph.15754>.
- Powell, J.R., Karunaratne, S., Campbell, C.D., Yao, H., Robinson, L., Singh, B.K., 2015. Deterministic processes vary during community assembly for ecologically dissimilar taxa. *Nat. Commun.* 6, 8444. <https://doi.org/10.1038/ncomms9444>.
- Powell, J.R., Rillig, M.C., 2018. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol.* 220, 1059–1075. <https://doi.org/10.1111/nph.15119>.
- Preston, K.A., Cornwell, W.K., Denoyer, J.L., 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytol.* 170, 807–818. <https://doi.org/10.1111/j.1469-8137.2006.01712.x>.
- Pringle, A., Taylor, J., 2002. The fitness of filamentous fungi. *Trends Microbiol.* 10, 474–481. [https://doi.org/10.1016/S0966-842X\(02\)02447-2](https://doi.org/10.1016/S0966-842X(02)02447-2).
- Pugh, G.J.F., 1980. Strategies in fungal ecology. *Trans. Br. Mycol. Soc.* 75, IN1–IN14. [https://doi.org/10.1016/S0007-1536\(80\)80188-4](https://doi.org/10.1016/S0007-1536(80)80188-4).
- Pugh, G.J.F., Boddy, L., 1988. A view of disturbance and life strategies in fungi. *Proc. Roy. Soc. Edinb. Sect. B Biol. Sci.* 94, 3–11. <https://doi.org/10.1017/S0269727000007053>.
- Reich, P., Ellsworth, D., Walters, M., Vose, J., Gresham, C., Volin, J., Bowman, W., 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80. [https://doi.org/10.1890/0012-9658\(1999\)080\[1955:GOLTRA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2).
- Reich, P.B., Tjoelker, M.G., Machado, J.-L., Oleksyn, J., 2006. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439, 457–461. <https://doi.org/10.1038/nature04282>.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U.S.A.* 94, 13730–13734.
- Riley, R., Salamov, A.A., Brown, D.W., Nagy, L.G., Floudas, D., Held, B.W., Levasseur, A., Lombard, V., Morin, E., Otiillar, R., Lindquist, E.A., Sun, H., LaButti, K.M., Schmutz, J., Jabbour, D., Luo, H., Baker, S.E., Pisabarro, A.G., Walton, J.D., Blanchette, R.A., Henrissat, B., Martin, F., Cullen, D., Hibbett, D.S., Grigoriev, I.V., 2014. Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc. Natl. Acad. Sci. U.S.A.* 111, 9923–9928. <https://doi.org/10.1073/pnas.1400592111>.
- Rineau, F., Roth, D., Shah, F., Smits, M., Johansson, T., Canbäck, B., Olsen, P.B., Persson, P., Grell, M.N., Lindquist, E., Grigoriev, I.V., Lange, L., Tunlid, A., 2012. The ectomycorrhizal fungus *Paxillus involutus* converts organic matter in plant litter using a trimmed brown-rot mechanism involving Fenton chemistry. *Environ. Microbiol.* 14, 1477–1487. <https://doi.org/10.1111/j.1462-2920.2012.02736.x>.
- Ritz, K., Crawford, J., 1990. Quantification of the fractal nature of colonies of *Trichoderma viride*. *Mycol. Res.* 94, 1138–1141. [https://doi.org/10.1016/S0953-7562\(09\)81346-4](https://doi.org/10.1016/S0953-7562(09)81346-4).
- Savage, V.M., Deeds, E.J., Fontana, W., 2008. Sizing up allometric scaling theory. *PLoS Comput. Biol.* 4, e1000171. <https://doi.org/10.1371/journal.pcbi.1000171>.
- Schrodt, F., Kattge, J., Shan, H., Fazayeli, F., Joswig, J., Banerjee, A., Reichstein, M., Bönsch, G., Díaz, S., Dickie, J., Gillison, A., Karpatne, A., Lavorel, S., Leadley, P., Wirth, C.B., Wright, I.J., Wright, S.J., Reich, P.B., 2015. BHPMF – a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Glob. Ecol. Biogeogr.* 24, 1510–1521. <https://doi.org/10.1111/gcb.12335>.
- Shah, F., Nicolás, C., Bentzer, J., Ellström, M., Smits, M., Rineau, F., Canbäck, B., Floudas, D., Carleer, R., Lackner, G., Braesel, J., Hoffmeister, D., Henrissat, B., Ahren, D., Johansson, T., Hibbett, D.S., Martin, F., Persson, P., Tunlid, A., 2016. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytol.* 209, 1705–1719. <https://doi.org/10.1111/nph.13722>.
- Simpson, G.G., 1944. *Tempo and Mode in Evolution*. Columbia Univ. Press., New York.
- Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale. *Ecol. Lett.* 11, 1252–1264. <https://doi.org/10.1111/j.1461-0248.2008.01245.x>.
- Sinsabaugh, R.L., Manzoni, S., Moorhead, D.L., Richter, A., 2013. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. *Ecol. Lett.* 16, 930–939. <https://doi.org/10.1111/ele.12113>.
- Smith, C.C., Fretwell, S.D., 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108, 499–506. <https://doi.org/10.1086/282929>.
- Smith, G.R., Steidinger, B.S., Bruns, T.D., Peay, K.G., 2018. Competition–colonization tradeoffs structure fungal diversity. *ISME J.* 12, 1758. <https://doi.org/10.1038/s41396-018-0086-0>.
- Smith, S.A., Brown, J.W., 2018. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* 105, 302–314. <https://doi.org/10.1002/ajb2.1019>.
- Smith, S.A., Brown, J.W., Hinchliff, C.E., 2013. Analyzing and synthesizing phylogenies using tree alignment graphs. *PLoS Comput. Biol.* 9, e1003223. <https://doi.org/10.1371/journal.pcbi.1003223>.
- Snajdr, J., Dobiašová, P., Větrovský, T., Valášková, V., Alawi, A., Boddy, L., Baldrian, P., 2011. Saprotrophic basidiomycete mycelia and their interspecific interactions affect the spatial distribution of extracellular enzymes in soil. *FEMS Microbiol. Ecol.* 78, 80–90. <https://doi.org/10.1111/j.1574-6941.2011.01123.x>.
- Southwood, T.R.E., 1988. Tactics, strategies and templets. *Oikos* 52, 3–18. <https://doi.org/10.2307/3565974>.
- Staddon, P.L., Ramsey, C.B., Ostle, N., Ineson, P., Fitter, A.H., 2003. Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of ¹⁴C. *Science* 300, 1138–1140. <https://doi.org/10.1126/science.1084269>.
- Steele, G.C., Trinci, A.P.J., 1975. The extension zone of mycelial hyphae. *New Phytol.* 75, 583–587. <https://doi.org/10.1111/j.1469-8137.1975.tb01424.x>.
- Steidinger, B.S., Crowther, T.W., Liang, J., Nuland, M.E.V., Werner, G.D.A., Reich, P.B., Nabuurs, G., de-Miguel, S., Zhou, M., Picard, N., Herault, B., Zhao, X., Zhang, C., Routh, D., Peay, K.G., 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* 569, 404. <https://doi.org/10.1038/s41586-019-1128-0>.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ, USA.
- Swenson, N.G., 2014. Phylogenetic imputation of plant functional trait databases. *Ecography* 37, 105–110. <https://doi.org/10.1111/j.1600-0587.2013.00528.x>.
- Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Funct. Ecol.* 22, 955–963. <https://doi.org/10.1111/j.1365-2435.2008.01402.x>.
- Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., Eerlandson, S., Vilgalys, R., Liao, H.-L., Smith, M.E., Peay, K.G., 2014. Endemism and functional convergence across the North American soil microbiome. *Proc. Natl. Acad. Sci.* 111, 6341–6346. <https://doi.org/10.1073/pnas.1402584111>.
- Talbot, J.M., Martin, F., Kohler, A., Henrissat, B., Peay, K.G., 2015. Functional guild classification predicts the enzymatic role of fungi in litter and soil biogeochemistry. *Soil Biol. Biochem.* 88, 441–456. <https://doi.org/10.1016/j.soilbio.2015.05.006>.
- Taylor, D.L., Walters, W.A., Lennon, N.J., Bochicchio, J., Krohn, A., Caporaso, J.G., Pennanen, T., 2016. Accurate estimation of fungal diversity and abundance through improved lineage-specific primers optimized for illumina amplicon sequencing. *Appl. Environ. Microbiol.* 82, 7217–7226. <https://doi.org/10.1128/AEM.02576-16>.
- Tedersoo, L., Bahram, M., Pölme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K.,

- Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., Kesel, A.D., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. *Science* 346, 1256688. <https://doi.org/10.1126/science.1256688>.
- Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.* 99, 1299–1307. <https://doi.org/10.1111/j.1365-2745.2011.01867.x>.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press.
- Tischer, A., Potthast, K., Hamer, U., 2014. Land-use and soil depth affect resource and microbial stoichiometry in a tropical mountain rainforest region of southern Ecuador. *Oecologia* 175, 375–393. <https://doi.org/10.1007/s00442-014-2894-x>.
- Tomkins, R.G., 1932. Measuring growth: the petri dish method. *Trans. Br. Mycol. Soc.* 17, 150–153. [https://doi.org/10.1016/S0007-1536\(32\)80033-1](https://doi.org/10.1016/S0007-1536(32)80033-1).
- Treseder, K.K., Lennon, J.T., 2015. Fungal traits that drive ecosystem dynamics on land. *Microbiol. Mol. Biol. Rev.* 79, 243–262.
- Trinci, A.P.J., 1974. A study of the kinetics of hyphal extension and branch initiation of fungal mycelia. *Microbiology* 81, 225–236. <https://doi.org/10.1099/00221287-81-1-225>.
- van der Heijden, M.G.A., Streitwolf-Engel, R., Riedl, R., Siegrist, S., Neudecker, A., Ineichen, K., Boller, T., Wiemken, A., Sanders, I.R., 2006. The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. *New Phytol.* 172, 739–752. <https://doi.org/10.1111/j.1469-8137.2006.01862.x>.
- van der Wal, A., Ottosson, E., Boer, W. de, 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology* 96, 124–133. <https://doi.org/10.1890/14-0242.1>.
- van der Wal, A., Klein Gunnewiek, P.J., Cornelissen, J.H.C., Crowther, T.W., de Boer, W., 2016. Patterns of natural fungal community assembly during initial decay of coniferous and broadleaf tree logs. *Ecosphere* 7, e01393.
- Voříšková, J., Baldrian, P., 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. *ISME J.* 7, 477–486. <https://doi.org/10.1038/ismej.2012.116>.
- Waksman, S.A., 1922. A method for counting the number of fungi in the soil. *J. Bacteriol.* 7, 339–341.
- Waldrop, M.P., Zak, D.R., Blackwood, C.B., Curtis, C.D., Tilman, D., 2006. Resource availability controls fungal diversity across a plant diversity gradient. *Ecol. Lett.* 9, 1127–1135. <https://doi.org/10.1111/j.1461-0248.2006.00965.x>.
- Walters, M.B., Reich, P.B., 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* 81, 1887–1901. [https://doi.org/10.1890/0012-9658\(2000\)081\[1887:SSNSAG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1887:SSNSAG]2.0.CO;2).
- Weichert, M., Fleißner, A., 2015. Anastomosis and heterokaryon formation. In: van den Berg, M.A., Maruthachalam, K. (Eds.), *Genetic Transformation Systems in Fungi*, vol. 2. Fungal Biology. Springer International Publishing, Cham, pp. 3–21. https://doi.org/10.1007/978-3-319-10503-1_1.
- Werner, G.D.A., Kiers, E.T., 2015. Partner selection in the mycorrhizal mutualism. *New Phytol.* 205, 1437–1442. <https://doi.org/10.1111/nph.13113>.
- West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276, 122–126. <https://doi.org/10.1126/science.276.5309.122>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Systemat.* 33, 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>.
- Wood, J., Tordoff, G.M., Jones, T.H., Boddy, L., 2006. Reorganization of mycelial networks of *Phanerochaete velutina* in response to new woody resources and collembola (*Folsomia candida*) grazing. *Mycol. Res.* 110, 985–993. <https://doi.org/10.1016/j.mycres.2006.05.013>.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827. <https://doi.org/10.1038/nature02403>.
- Zanne, A., Abarenkov, K., Afkhami, M., Aguilar-Trigueros, C., Bates, S., Bhatnagar, J., Busby, P., Christian, N., Cornwell, W., Crowther, T., Flores-Moreno, H., Floudas, D., Gazis, R., Hibbett, D., Kennedy, P., Lindner, D., Maynard, D., Milo, A., Nilsson, R., Powell, J., Schildhauer, M., Schilling, J., Treseder, K., (in press). Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biol. Rev.*
- Zeilinger, S., Gupta, V.K., Dahms, T.E.S., Silva, R.N., Singh, H.B., Upadhyay, R.S., Gomes, E.V., Tsui, C.K.-M., Nayak S. C., 2016. Friends or foes? Emerging insights from fungal interactions with plants. *FEMS Microbiol. Rev.* 40, 182–207. <https://doi.org/10.1093/femsre/fuv045>.
- Zhang, J., Elser, J.J., 2017. Carbon:Nitrogen:Phosphorus stoichiometry in fungi: a meta-analysis. *Front. Microbiol.* 8 <https://doi.org/10.3389/fmicb.2017.01281>.