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1 **Branching out: towards a trait-based understanding of fungal ecology**

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20

21 **Abstract**
22
23 Fungal ecology lags behind in the use of traits (i.e. phenotypic characteristics) to understand

24 ecological phenomena. We argue this is a missed opportunity and that the selection and systematic

25 collection of trait data throughout the fungal kingdom will reap major benefits in ecological and

26 evolutionary understanding of fungi. To develop our argument, we first employ plant trait examples

27 to show the power of trait-based approaches in understanding ecological phenomena such as

28 identifying species allocation resources patterns, inferring community assembly and understanding

29 diversity-ecosystem functioning relationships. Second, we discuss ecologically relevant traits in fungi

30 that could be used to answer such ecological phenomena and can be measured on a large proportion

31 of the fungal kingdom. Third, we identify major challenges and opportunities for widespread,

32 coordinated collection and sharing of fungal trait data. The view that we propose has the potential to

33 allow mycologists to contribute considerably more influential studies in the area of fungal ecology

34 and evolution, as has been demonstrated by comparable earlier efforts by plant ecologists. This

35 represent a change of paradigm, from community profiling efforts through massive sequencing tools,

36 to a more mechanistic understanding of fungal ecology.

37 **Keywords:**

38   Traits; resource allocation; community assembly; ecosystem processes

39

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1. Introduction

We live in a fungal world (de Boer et al., 2005); fungi profoundly impact population, community and ecosystem dynamics from local to global scales (Averill et al., 2014; Fisher et al., 2012). Yet fungal ecologists struggle to comprehensively understand fungal community assembly and its contribution to ecosystem functioning. Such understanding requires knowledge of the traits (i.e. phenotypic characteristics) of species that determine both their responses to environmental factors and their effect on ecosystem processes (Mcgill 2006; Petchey and Gaston 2006). So far, fungal traits have been used mainly for identification and classification (Kumar et al., 2011) but rarely for understanding fungal ecology. We argue that the selection and systematic collection of trait data throughout the fungal kingdom will reap major benefits in ecological and evolutionary understanding of fungi.

In this paper, we highlight how a core set of fungal traits can be used to address ecological phenomena. To do this, we employ plant trait examples, where the trait approach has been used successfully (e.g. Katabuchi et al., 2012). Second, we exemplify ecologically relevant traits in fungi, focusing on traits that can be measured for a large proportion of the fungal kingdom. Third, we identify major challenges and opportunities for widespread, coordinated collection and sharing of fungal trait data.

2. Using trait data in ecological research: examples from plant ecology

Trait data have been used in ecology for different purposes, but here we concentrate on three influential examples of the use of a core set of plant traits as a means of (i) identifying trade-offs in resource use, (ii) detecting the relative importance of habitat filter versus niche partitioning in community assembly, and (iii) understanding how biodiversity affects ecosystem processes by quantifying functional diversity. We focus on plant ecology because this field presents the most thorough development of a trait-based ecology (Adler et al., 2013) and provides examples analogous to many aspects of fungal biology.

(I) Identifying trade-offs in resource use.

Trait data can be used to identify patterns of resource allocation to fitness components and physiological functions (Westoby et al., 2002). In a landmark study, Wright et al. (2004) used six leaf traits to show that plant species can be placed along a major axis in the revenue obtained per leaf construction unit, which they termed the "leaf economic spectrum": at one extreme, there are species that invest few resources in leaf construction (e.g. thinner leaf, blade, shorter leaf lifespan) with short-term gains in photosynthates, while other species

77		exhibit the opposite trait combinations (e.g. thicker leaf blades, longer leaf lifespan). This
78		spectrum is consistent across a wide range of habitats, latitudes, and ecosystem types.
79		
80	*(II)*	Detecting the relative importance of habitat- filtering versus niche- partitioning in community
81		assembly.
82		These approaches are based on measurements of trait means, variances and ranges at the
83		community level. For example, habitat filtering (i.e., the extent to which abiotic factors like
84		temperature, pH or nutrient levels prevent some species from establishing in local
85		communities (HilleRisLambers et al., 2012)) is indicated by reductions in the trait ranges at
86		local scales. The rationale is that some species (and their traits) will be excluded in local
87		communities with particular environmental conditions, and thus the trait range at local scales
88		will be smaller than expected by chanceas most species will have similar trait values
89		(Cornwell et al., 2006). For example, in low resources nutrient patches (light, mineral
90		nutrients) small-seeded plants -cannot establish given the fewerlower amount of reserves
91		they possess in comparison to large-seeded plantswill be excluded, thus the observed as only
92		the large-seeded subset of the species pool can establish, the lower the range of seed sizes
93		observed in the patch more large-seeded species establish on such patches, the range of
94		seed sizes (the difference between the largest and smallest seed) in the community would be
95		smaller (see (Kraft and Ackerly, 2010) for details on statistical analysis). sizein local low
96		nutrient patches will be small (Adler et al., 2013). At the other extreme, niche partitioning
97		(i.e. the extendt byto which interacting species differ in their niches to stabstablyle co-exist)
98		is inferred from increasing dissimilarities in trait values among co-occurring species (,
99		especially of traits related to -the way they obtain resources acquisition, and deal with stress
100		and enemy attack). Thus, trait values among co-occurring species would be expected to be
101		more different than expected by chance (Paine et al., 2011). For example, it has been shown
102		that when plant species interact, they have dissimilar rooting depth values, reflecting
103		partitioning of soil resources (Nobel, 1997)). Thus, niche partitioning is inferred from over-
104		dispersion in trait values among co-occurring species that iswould be expected to be more
105		different greater than expected by chance (Paine et al., 2011) indicating reduced niche
106		overlap (Adler et al., 2013).
107		
108	*(III)*	Understanding how biodiversity affects ecosystem processes by quantifying functional
109		diversity.
110		Functional diversity refers to the number of functionally different speciesspecies present in a
111		community. The particular "function" a species performs is reflected by the sum of all the is

112 operationalized as pair-wise distances in trait values between species occurring in local
113 communities in an *n*-dimensional trait space. The traits considered are chosen as those most
114 likely to traits it possess that reflect determine the its contribution of species to an the
115 ecosystem process in question of interest (Petchey and Gaston, 2006). In plants, resource
116 acquisition traits are commonly used (e.g., plant height reflects the ability to intercept light;
117 leaf nitrogen concentration reflects the ability to acquire nitrogen). Further, multivaritate
118 statistical metrics have been developed to that capture differences between species
119 occurring in a given community using multiple traits (Petchey and Gaston, 2002). Functional
120 diversity defined in this way by plant traits has been shown to be a better predictor of, for
121 example, aboveground productivity than other measures of diversity such as species richness
122 (e.g. Flynn et al., 2011).
123
124
125 **3. Defining ecologically relevant fungal traits**

126 In this section we identify the types of fungal traits that are good candidates for trait-based
127 approaches mentioned in the previous section based on three criteria: (1) *ecological versatility of*
128 *traits*, i.e. the traits should be representative for inferring fungal use of resources, community
129 assembly mechanisms and multiple ecosystem processes, (2) a *wide scope throughout the fungal*
130 *kingdom, i.e.* the traits should be relevant for a large pool of fungal species, and (3) *measurability*, i.e.
131 methods should exist (or can be conceived) for their standardized measurement. In this way, data
132 can be obtained from a large pool of species in a relatively short time using standardized protocols.

133 *3.1 Ecological versatility of traits*

134 Traits meeting this criterion (Table 1) are grouped into life-history, morphological or physiological
135 traits. Life-history traits reflect resources investment into different fitness components: survival,
136 growth and reproduction (Flatt and Heyland, 2011). For example, life span of hyphae/fungal
137 structures, number of spores/propagules, and allocation of number biomass of either vegetative
138 hyphae mycelia or reproductive structures represent fungal life history traits.
139 The morphological and physiological traits should correlate with fitness components, have predictive
140 value in explaining species responses to environmental factors, or be relevant for ecosystem
141 processes. Unlike plant trait data for which empirical support has been established (Westoby et al.,
142 2002), the ecological relevance for many fungal traits are based on expert opinion and have yet to be
143 empirically tested.
144 We summarize the potential relevance of some of the traits in community assembly and ecosystem
145 functioning in Table 2. For community assembly, any trait that can be related to a major ecological

146 axis such as resource acquisition, enemy avoidance (predation/fungivory), or stress tolerance (Chase
147 and Leibold, 2003) may be useful. As fungi are involved in many ecological processes, an exhaustive
148 list of fungal functional traits impacting ecosystem processes is beyond the scope of the paper.
149 Instead we illustrate three key ecosystem processes for which we expect fungi to play an important
150 role in terrestrial ecosystems: soil aggregation, plant productivity (host growth) and organic matter
151 decomposition (Boddy, 2001; Mitchell, 2003; Rillig et al., 2014). Some of the traits, such as those
152 related to mycelial architecture, may be linked to several ecosystem processes (Table 2).
153
154 *3.2 Scope of the traits within the fungal kingdom*
155 The traits in Table 1 are mostly applicable to terrestrial, filamentous fungi. We consider this group as
156 a good starting point in the development of a trait-oriented approach because they include the
157 largest known diversity of the fungal kingdom, exhibit a wide variety of lifestyles, and have a
158 cosmopolitan distribution (Blackwell, 2011). However, traits relevant for aquatic and non-filamentous
159 basal fungi require further consideration (Stajich et al., 2009).
160
161 *3.3 Measurability of the traits*
162 Traits are measured on individuals, but the modular growth of filamentous fungi challenges
163 definitions of what an individual is (Pringle and Taylor, 2002); here we propose trait measurements of
164 fungal structures (e.g. hyphae, spores) important in colonizing a~~a~~ resource patch. A resource patch can
165 be operationalized as a unit of host plant tissue, decaying material, or a Petri dish with a known
166 medium under a narrow set of environmental conditions. This approach is aligned with models of
167 fungal resource allocation (to mycelial growth vs. spore production), and focuses on the number or
168 size of fungal structures within a resource patch (Gilchrist et al., 2006). Furthermore,
169 ~~measruing~~measuring~~focusing on~~ fungal traits ~~found under given~~~~within resource patches~~on controlled
170 conditions allows the standardization of trait measurements and the integration of existing data from
171 the literature and databases on fungal growth rates on different substrates/media (discussed below).
172 In fungi, data obtained under such controlled environmental conditions have great potential for
173 understanding ecological phenomena, as exemplified by the use of plant relative growth rate
174 (measured in hydroponic conditions) to predict productivity in the field (Vile et al., 2006).

175 **4. Overcoming challenges to facilitate the widespread use of trait approaches in fungal**
176 **ecology**

177 *4.1. Trait data collection*

178 Currently, fungal trait measurements are made in a non-systematic fashion with a variety of
179 protocols, often focusing on qualitative, rather than quantitative, differences and with taxonomic
180 purposes. For instance, recent metabolic surveys of fungi measured enzyme activity using a variety of
181 methods (as e.g. in Mandyam et al. (2010); or in Promputtha et al. (2010)). No "handbooks" exist for
182 the measurement of ecologically relevant fungal traits as do for plants (e.g. Pérez-Harguindeguy et
183 al., 2013). Such handbooks would provide an important resource for mycologists and additionally
184 serve as a teaching tool. Undergraduate courses in mycology represent an excellent opportunity to
185 obtain trait data from cultured isolatess and environmental samples.

186 *4.2. Use of intraspecific trait diversity*

187 Most trait-based ecological studies for plants consider the species as the unit of interest. This results
188 in the practice of using average trait values per species, often ignoring intraspecific trait variability
189 (e.g. Kraft et al., 2011). However, incorporating this source of variability could lead to improved
190 predictability (Bolnick et al., 2011; Violle et al., 2012). In fungi, intraspecific trait variability is
191 expected to be high (Behm and Kiers, 2014), given inherent intraspecific variability, trait plasticity in
192 different environments/hosts or complex saprotrophic-symbiotic cycles (Rodriguez et al., 2009).
193 Methods have been proposed to incorporate intraspecific variability when measuring functional
194 diversity (de Bello et al., 2011) and community ecology studies incorporate intraspecific variability to
195 better understand community assembly (e.g. Jung et al., 2010). Therefore, an additional challenge
196 will be to incorporate the life-cycle diversity of ecologically relevant traits in fungi.
197
198 *4.3. Storage and availability of trait data*

199 Currently, there is a wealth of valuable fungal trait data in culture collections, taxonomic keys and
200 compendia. These data are often stored in a variety of formats and accessibility. These include
201 mycological journals with species descriptions, compendia for identification of fungi (e.g. Domsch et
202 al., 2007), and laboratory records of individual mycologists. Collating and making such data available
203 should be a primary task. In addition, specialized databases are scattered over a different locations,
204 using different formats. Examples are the AFTOL structural and biochemical fungal trait databases
205 (https://aftol.umn.edu/), the CBS fungal growth on media/substrate database (http://www.fung-
206 growth.org/), and the fungal plant cell-wall degrading enzyme database
207 (http://pcwde.riceblast.snu.ac.kr). A global trait database for fungal ecology is a long-term goal and
208 the immensity of this task should not intimidate researchers. Initially, plant trait data were similarly
209 disparte and it took several years before they were successfully aggregated into comprehensive
210 databases (Kattge et al. (2011).
211

4.4. Linkage to genomic data

Mycologists are inventorying fungal species using genomic methods at a massive scale in a multitude of ecosystems. The wealth of fungal genomic data obtained by this high-throughput sequencing is underused in terms of asking general ecological questions (Poisot et al., 2013), nor is it being linked to ecological relevant fungal traits. However, these DNA-based species have no corresponding morphotype; and thus there is little knowledge of what changes in species compositions means in terms of functional, or trait properties of communities (Prosser et al., 2007). If this wealth of information could be linked to a functional trait database, data generated in high-throughput sequencing could be used to better understand fungal community assembly and its relationship ecosystem processes. A trait database could be linked to genetic barcodes (the choice of which has recently been agreed upon for fungi (Kõljalg et al., 2013; Schoch et al., 2012), and integrated with taxonomic databases such as UNITE and DEEMY for ectomycorrhizal fungi (Abarenkov et al., 2010; Agerer and Rambold, 2004). Clearly, concerted and co-ordinated characterization of fungi with regard to genomics, phylogenetics and traits is a major opportunity.

5. Concluding remarks

Among mycologists, efforts are increasing to implement trait-based approaches both conceptually (Aguilar-Trigueros et al., 2014; Crowther et al., 2014; Chagnon et al., 2013; Falconer et al., 2011; Koide et al., 2014) and empirically (Pena and Polle, 2014; Philibert et al., 2011). While these efforts have been valuable, their scope has been limited to defined functional groups (e.g., root-associated fungi, forest pathogens) or specific interactions (e.g., competition). We propose to build on these approaches. This process represents a change of paradigm, from community profiling efforts through sequencing tools and a focus on species composition to a more intimate, deeper understanding of fungi in ecosystems. This mechanistic understanding will allow key ecological questions to be addressed including, for example: What are the consequences of fungal diversity loss in terms of ecosystem functioning? Can we predict fungal community change due to climate or land-use change? Can we manipulate fungal communities to better support ecosystem services?

Field Code Changed	

249

250

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