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Commentary

Back to the future: natural history and the way forward in modern fungal ecology

ABSTRACT

The growing power and increasing availability of molecular tools for identifying fungi in environmental samples has revolutionized the way that fungal ecologists work. As a result, more people from around the globe have jumped into the fungal community sequencing endeavor. Paradoxically, as these extensive datasets accumulate we are often at a loss for interpretation due to the lack of basic autecology and natural history information for most fungi. As a result we are in danger of learning less and about more and more. I suggest that one way forward in fungal ecology is through a modern version of fungal natural history, with a focus on holistic understanding of individual species and ecosystems, but driven by modern genomic and molecular tools. By combining the extensive data generated through environmental sequencing with an intensive, molecular-based natural history we can create a synergy that will propel fungal ecology forward.

The growing power and increasing availability of molecular tools for identifying fungi in environmental samples has revolutionized the way that fungal ecologists work (Horton and Bruns 2001; Lindahl et al. 2013). We are now able to identify the presence of hundreds of co-existing species in minute samples of soil (<1 g) or plant tissue. More importantly, we are able to do this at a throughput – both in terms of sequence depth per sample (10,000 s) and number of samples (100 s) – at a per sample cost (<$10) that was unimaginable just a few years ago, when the first next generation sequencing (NGS) platforms hit the market (Fig 1). As a result, more people from around the globe have jumped into the fungal community sequencing endeavor, generating large datasets from the rainforest (McGuire et al. 2012) to the bottom of the ocean (Orsi et al. 2013) and from the skin on our backs (Findley et al. 2013) to the air that we breathe (Adams et al. 2013). These same tools have reconfigured the study of other 'microbial' groups where morphological taxonomy is of limited use – such as bacteria and viruses. From the pace of microbial discovery it is easy to draw parallels to the naturalist frenzy of 18th century Europe, when scientists like Linnaeus and Buffon were trying to collect and classify the visible dimensions of diversity on our planet.

As we synthesize results from across studies, and large scale sequencing efforts come to fruition, we are learning important things about the diversity and distribution of fungi at both small and large spatial scales. For example, contrary to previous expectations (Bisby 1943), most fungi are not cosmopolitan and have restricted geographic ranges (Kivlin et al. 2011; Sato et al. 2012; Meiser et al. 2013; Talbot et al. in press). Similarly, interesting large-scale diversity patterns are emerging. For example, ectomycorrhizal fungi appear to peak in diversity at mid-latitudes rather than the tropics (Tedersoo et al. 2012). Similar non-canonical patterns have been found in bacteria (Fierer et al. 2011), raising the question of whether the climate variables that correlate with macro-organism diversity are truly general factors controlling all organismal diversity. At smaller scales, we find that fungal diversity varies dramatically across habitats, from hundreds of species in a few grams of soil (Peay et al. 2013), to dozens of endophytes in a single tree (Zimmerman and Vitousek 2012) and near monodominance by single species of yeast in floral nectar (Beslisle et al. 2011). These discoveries raise important questions about the fundamental processes that control fungal diversity and distributions and how the unique biology of fungi contributes to generating the patterns we observe.

Despite all of this information, publication of fungal NGS studies appears to have lagged behind 16S studies of bacterial communities. For example, the search term "ecology" in the GenBank Short Reads Archive (Dec 2013) turned up 150 studies, of which 51 are bacterial and four are fungal. This may be, in part, because of the comparative difficulties in analyzing fungal ITS datasets, due to the lack of a standardized bioinformatics pipeline. However, with the incorporation of fungi into the QIIME platform tutorials (Caporaso et al. 2010), some recent papers on NGS guidelines (Nilsson et al. 2011; Lindahl et al. 2013) and the generation of a well curated ITS database (Kõljalg et al. 2013), the pace of dataset publication should increase rapidly. One consequence of this standardization and low-cost sequencing is that scientists without a background in mycology appear to be increasingly incorporating fungi into their research. This democratization of molecular techniques has eroded many of the taxonomic and methodological barriers that traditionally separated microbiologists and ecologists of various stripes. In particular, people traditionally working on bacterial communities are well poised to integrate fungal communities into their data streams. Perhaps not surprisingly, the ability to use molecular tools to detect fungi quickly and easily has likely been part of the growing

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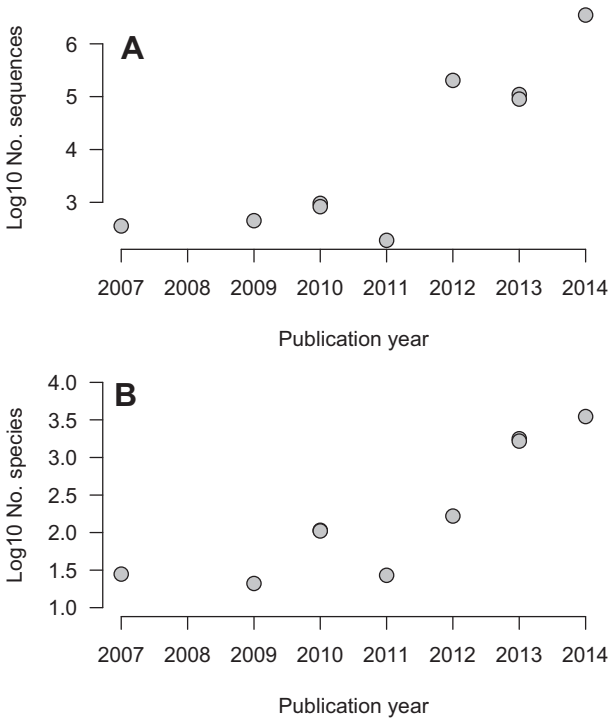

Fig 1 – A personal sequencing journey. Improving technologies are dramatically increasing the number of DNA sequences obtained and number of species detected in fungal community studies. Figure shows (A) the number of sequences obtained for fungal community ecology studies published by the author starting in 2007 up to the present. Most recent data point is an unpublished manuscript in process based on runs on the Illumina MiSeq platform; (B) the corresponding increase in the number of species uncovered with higher throughput methods. The increase in sequences and species richness makes unraveling the ecology of fungal communities evermore difficult without more autecological context.

appreciation of the fungal role in shaping ecosystems (e.g. Fisher et al. 2012; Liu et al. 2012; Clemmensen et al. 2013).

As should be clear from the previous paragraphs, all of these developments are having a positive effect on the field of fungal ecology. In some ways it is tempting to declare victory – we have the tools we always dreamed about and growing recognition of fungal importance amongst scientists and the general public. However, as conquering armies sometimes learn, winning the peace can be more difficult than winning the war. What do I mean by this? For the last two decades, arguably the biggest limit on our knowledge about fungal communities appeared to be sequencing power. That limit is now disappearing or gone. For even longer, academic mycologists were the majority of people that cared about fungal ecology. That is no longer the case. While these are both positive developments, I also think it indicates that the field may be approaching a crossroads. In a new age of unlimited sequencing power and widespread scientific participation, what is the most productive way to push fungal ecology forward?

There are, of course, many (and by no means mutually exclusive) paths that will move the field forward. The current trend appears to be riding the wave of increasing sequencing power to characterize fungal communities from a greater diversity of environments and at greater sequencing depth than previously possible. Metagenomics, metatranscriptomics (Baldrian et al. 2012), and even meta-proteomics (Schneider et al. 2012) will soon be providing an increasingly rich data stream for fungal ecologists to mine. This approach is certainly important, but it has limitations and will eventually reach the point of diminishing returns. This is primarily because environmental metagenomics *sensu lato* is an extensive source of data, rather than intensive source of data.

I say this for a number of reasons. First, Next generation amplicon sequencing of barcode genes can produce very comprehensive profiles of fungal community structure. However, we know the identity of most operational taxon units (OTUs) used in molecular studies only imprecisely and the usual blanket 97 % sequence similarity cutoffs used to delineate OTUs may obscure meaningful ecological differences (Kõljalg et al. 2013). In addition, the relationship between gene abundance and organismal abundance is not direct (Amend et al. 2010; Baldrian et al. 2012). Even with better algorithms and databases for taxonomic assignment, we still know very little about the detailed ecology of even OTUs for which a clear taxonomic assignment can be made. Well-designed sequencing studies can tell us a lot about the spatial distribution of fungi, but there is an important interplay between interpreting environmental sequencing and *a priori* knowledge of organismal ecology. For example, Lindahl et al. (2007) showed in a very elegant study that there was a strong correlation between the age of soil carbon substrates and the distribution of ectomycorrhizal and saprotrophic fungi. However, the most powerful conclusions from this work were based on *a priori* ecological knowledge that allowed the assignment of OTUs to trophic guilds, and even in this case only 25 % of the identified fungi could be thus assigned. Difficulty assigning trophic guild is not an uncommon problem, despite the fact that trophic mode is perhaps the most fundamental feature of an organism. A pioneering study by Vandenkoornhuyse et al. (2002) was unable to assign trophic guild for 94 % of the root-associated fungi they detected. This problem has only grown as NGS studies uncover greater and greater fungal diversity.

At some point the ecological detail we can learn from the OTU × sample data matrices (i.e. OTU tables) generated through NGS studies is limited, regardless of how good the environmental metadata is. This limit exists because the information in an OTU table is ultimately static – OTU tables tell us little directly about the nature of the interactions going on between the organisms present and between the organisms and their environment. For example, a significant portion of the fungal community detected through DNA sequencing may not even be metabolically active. Baldrian et al. (2012) found significant differences in the fungal community when sequencing DNA compared with RNA, suggesting that DNA is not an accurate representation of metabolic activity. Similarly, Nguyen (Pers Comm) has found that ectomycorrhizal spores buried in a closed container without host roots (i.e. no active hyphae could develop) could be amplified

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and sequenced from soil even 5 yr later. While this may be advantageous for some situations (e.g. it effectively extends the spatial and temporal window of sampling), it can also be misleading as taxa may persist passively as spores in environments totally different from the ones in which they eventually germinate and grow. While statistical approaches can help infer these interactions from co-occurrence patterns (Barberan et al. 2012) or changes in community structure across environmental gradients (Polme et al. 2013), this knowledge is indirect. Similarly, functional genes or RNA may give a better picture of overall community function, but it is currently not possible to link genes back to individual organisms and most of the data from these approaches is currently uninterpreted. As a result, the high throughput approach to fungal ecology teaches us a little individually about a lot of organisms.

While there is value in the large sum of information generated through the extensive approach, I believe that we should simultaneously be encouraging an equally significant investment in an *intensive* approach to fungal ecology. I will first describe what I think constitutes an intensive approach, describe how I think it can benefit fungal ecology, and then suggest some questions that may serve as a starting points in this endeavor. In essence, the intensive approach to fungal ecology means learning more biological detail about fewer organisms and places. First, this approach should be species-centric. Before we can truly understand fungal communities, we need to understand the autoecology of individual species (Gleason 1926). Only by doing this can we interpret ecological studies realistically. This effort should harness modern molecular and genomic tools to uncover in detail the individual life history strategies, key ecological interactions, functional capabilities and niche dimensions for fungal species. Since this can never be done for the likely upwards of five million fungal species on the planet (Blackwell 2011; Taylor et al. 2014), it should focus on 'important' species. While importance is subjective, some species have a large impact in their local communities (e.g. large fraction of biomass, perform key functions) or may be representative of a large number of species (e.g. particular clades). While it might seem like our knowledge in this dimension would be sufficient, we still do not know key biological details for entire groups of fungi – for example, it is still unclear what induces spore germination for many ectomycorrhizal fungi (Miller et al. 1993) or even precisely what roles spore dispersal plays in their lifecycle. In the cases where these kinds of ecological detail are being investigated we are learning surprising things. For example, the main vegetative growth phase of most Agaricomycetes is thought to initiate soon after spore germination when haploid hyphae fuse leading to formation of a dikaryon. While we might expect the nuclei originating from each haploid spore to have even abundance within the mycelium, recent work has shown that, in some species, these haploid nuclei compete with each other (James et al. 2009). This can lead to highly imbalanced nuclear ratios in the mycelium and raises questions about the mechanisms of nuclear competition and how genotype ratios affect mycelial phenotype. Similarly, there is some evidence that changes in the relative abundance of genetically distinct nuclei in arbuscular mycorrhizal fungi may allow for rapid genetic and phenotypic changes in response to novel environments (Angelard et al. 2014).

Second, the intensive approach should favor long-term, longitudinal studies in a single system. Only with repeated observations in a single place will the key ecological details of many species interactions become clear. For example, insights into the importance of the ectomycorrhizal spore bank for early seedling colonization was possible because of repeated surveys of a system before and after disturbance (Baar et al. 1999; Taylor and Bruns 1999; Bruns et al. 2002). Long-term studies and repeated samples are also critical for defining the complete pool of species that are present in a local system and the potential importance of infrequent events in structuring fungal communities.

Finally, this research should incorporate rigorous manipulative experiments guided by ecological theory. Building on observational studies, manipulative experiments can ultimately disentangle the key factors structuring fungal communities. For example, determining when co-occurrence patterns are caused by strong species interactions (Kennedy et al. 2011) or which variables are the primary factors structuring fungal communities across environmental gradients (Parrent et al. 2006). Similarly, ecological theory can help us to ask the right questions about what is important in fungal ecology. In my own work, the theory of island biogeography (MacArthur and Wilson 1967) has provided a critical framework to ask questions about how dispersal controls patterns of diversity and community structure in ectomycorrhizal fungi (Peay et al. 2012b). The approach I have outlined certainly carries some flavor of natural history, in the traditional sense of gaining a holistic appreciation for organisms and their place in the environment. However, I think a modern science of fungal natural history, driven by cutting edge molecular tools and guided by theory and experimentation, will have many potential benefits.

To start with, detailed work on the ecology of individual species will dramatically increase the value of extensive datasets. A deeper understanding of functional strategies will help to infer ecology from the species × sample data matrices (OTU tables) generated by NGS and may help explain much of the variation that remains unexplained in large community datasets. For example, functional trait composition may be more strongly correlated with environmental gradients than species composition *per se* if many species share similar trait syndromes (Chagnon et al. 2013). This may explain why enzyme activity of soil fungal communities (Kivlin and Treseder 2013) and wood decomposition rates (Peay et al. 2012a) may converge, even when species composition is very divergent. Deeper understanding of the genomes of individual species will also help to interpret true metagenomic or metatranscriptomic datasets by allowing better assignment of reads to organisms and by helping in assigning function to reads. However, assigning functional roles to species or genes based on assumptions of relatedness or homology runs the risk of compounding errors, unless there is a well-tested evolutionary framework available for understanding how fungal traits vary across phylogenetic scales.

Because the intensive approach draws on traditional mycological methods, it will also help to keep many key skills and infrastructure alive in the discipline. For example, it is

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critical that mycologists continue to know diagnostic morphological features associated with traditional taxonomy, are able to isolate and maintain organisms in culture, and maintain culture collections and herbaria. In addition, working directly with organisms serves as a constant reminder of the evolutionary and phylogenetic context in which these organisms exist. Keeping this skillset and perspective alive is important because pure mycology positions are relatively rare and many practicing mycologists are in faculty positions, as ecologists, molecular biologists or evolutionary biologists, where they do not teach mycology and actively use these fundamental skills. Finally, a holistic approach to fungal communities may also have many practical benefits. For example, a detailed understanding of the fungal community at one place may help in producing recommendations for land managers with regards to the fungal community, produce stronger ties with local interest groups (e.g. local mushroom pickers or mushroom clubs), or help in managing invasive species.

In the previous paragraphs I outlined some of the broad features and benefits of the intensive approach, but what are some specific research questions that might help shape this endeavor? Here are six questions that I think will be important:

(1) What are the primary axes of functional diversity along which local fugal communities are organized, both within and across guilds?
(2) Are there common trait combinations and how do these give rise to the emergent natural history of fungal species?
(3) When and at what evolutionary scale can we assume that a trait is conserved and when do we need to make independent measurements?
(4) What are the genes associated with major traits axes and what genomic features lead to species differences?
(5) How do natural histories of individual species give rise to the unique features of fungal communities?
(6) What are the new lab techniques and ecophysiological tools we need and the taxonomic groups we should focus on in order to expand the range of culture collections and experimentation?

Answering these questions will require genomic resources, field observations on fungal community membership, a renewed commitment to taxonomy, and the ability to conduct experiments that manipulate the abundance and diversity of key organisms. As we gain a modern understanding of fungal natural history, we will be poised to answer important questions in ecology and evolution. For example, how species diversity affects ecosystem function is central to ecology. While the focus has been on positive ecosystem-function relationships, there is evidence that increasing fungal diversity can decrease rates of wood decomposition (Fukami et al. 2010). Understanding why this is the case and when this effect will be important in natural systems requires answers from most of the questions listed above. First, it is critical to know what organismal traits affect the ecosystem process in question (Q1); for example, in wood decomposing communities, the ability to produce enzymes that break down cellulose and lignin. Knowing the genomic basis of these traits allows one to quantify changes in gene expression as more species are added or the identification of novel genes expressed during interspecific interactions that might affect decomposition related enzymes (Q4). Knowledge of life history strategies will help predict which species from the regional pool are actually likely to be present at a given stage of decay (Q2, Q5) and an evolutionary framework will help to predict what trait combinations these species represent (Q3). The ability to culture the organisms (Q6), manipulate diversity, and measure gene expression can provide direct tests about the mechanisms by which diversity affects organismal interactions and ecosystem process rates. In addition, detailed experimental work can help us move beyond the circularity of assigning function through GO and BLAST homology and discover new functional genes that control important phenotypes, such as modes of inter-specific competition (Q4). Answering these questions to arrive at a better understanding of when and why fungal diversity affects ecosystem function will be important well beyond the field of fungal ecology.

The molecular revolution is here to stay and by no means should we abandon the powerful tools it has brought us. However, for fungal ecology to move forward it also seems that we need to look back to the roots of the field. We are not alone in this need and other fields have also called for increased investment in natural history and associated infrastructure (Tewksbury et al. 2014). By combining the extensive data generated through the molecular revolution with an intensive, molecular natural-history, I think we can create a synergy that will propel fungal ecology forward.

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Kabir G. PEAY*

Department of Biology, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, USA

**Corresponding author*. Tel.: +1 650 723 0552; fax: +1 650 725 8221.
E-mail address: kpeay@stanford.edu

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