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Commentary

The use of artificial media in fungal ecology

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ABSTRACT

Can experiments conducted in agar really help us to understand the complexity of fungal systems? This question has been the focus of persistent and ongoing debate between fungal ecologists that favor reductionist versus holistic approaches. On one hand, artificial media are unrealistic and fail to reflect the heterogeneity and complexity of natural systems. But on the other hand, they offer simplified model systems that allow us to isolate mechanisms that would otherwise be obscured in natural systems. Following various technological advances that enable us to describe various aspects of complex fungal communities *in situ*, the dial appears to be tipping in favor of observational field studies, and the use of artificial media has declined. However, we argue that the loss of artificial media from experimental studies would impair our capacity to disentangle the complexities of fungal communities. Here, we discuss the pros and cons of artificial media in fungal ecology and outline the types of questions that are best addressed using fungi growing in artificial media. We conclude that renewed emphasis on the value of artificial media could help us to generate the mechanistic understanding that might be critical to explaining the exciting patterns that are emerging from real-world fungal ecology studies.

1. Introduction

Since the dawn of this research field fungal ecologists have been divided along a spectrum of approaches. Those favouring holistic approaches choose to observe fungal communities in natural systems, enabling the identification of real-world patterns that might be explained by theory. On the other end of the spectrum, reductionists prefer to use simplified model systems to examine ecological mechanisms that might underpin those important ecological patterns. Although manipulative field experiments can serve as an intermediate between these approaches (Crowther et al., 2015; Hiscox et al., 2015), the majority of studies in fungal ecology fit at either end of this spectrum. As with most biological fields, the combination of these approaches is the best way to provide conceptual depth and to build a mechanistic understanding of fungal dynamics (Peay, 2014; Vilanova and Porcar, 2016). However, following a wide range of technological advances (e.g. high-throughput sequencing, stable isotope and imaging techniques etc.) that enhance our capacity to describe fungal communities *in situ*, the scale has tipped drastically in favor of the holistic approaches, at the expense of mechanistic experimental studies (Peay, 2014; Vilanova and Porcar, 2016).

Traditionally, artificial media (ArtMed) such as solid agar or broth conditions have been used extensively as simplified model systems to perform manipulative experiments in fungal ecology (see Fig. 1). As such, much of the holistic versus reductionist debate has centered around experiments that make use of ArtMed. These model systems have been central to much of our basic understanding of fungal biology, providing a unique opportunity to observe fungi directly, and under highly controlled conditions. However, in search of increasing experimental realism, and facilitated by the emerging technological tools (e.g. genetic, stable isotope or remote sensing tools) there has been a concerted move away from the use of ArtMed in fungal experiments, towards natural substrates (e.g. plant roots, wood or soil) that more closely replicate natural systems (Fukami et al., 2010; Crowther et al., 2011a; Hiscox et al., 2015). Indeed, only 17% of the experimental studies published in *Fungal Ecology* in 2015 were conducted on artificial media, in comparison to 57% in 2010. As such, ArtMed are commonly being relegated to use as simple culture media. This declining use of ArtMed has pervaded the entire field of microbial ecology.

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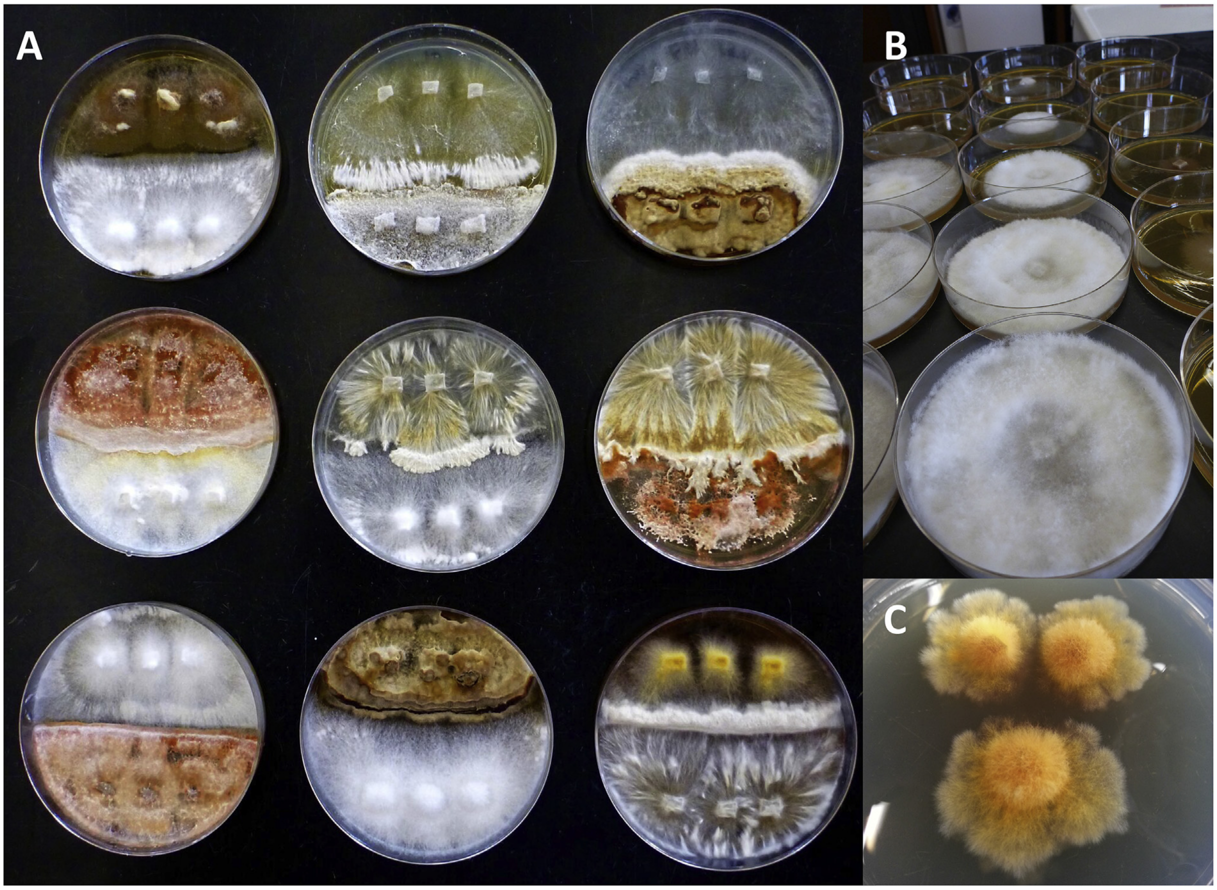

Fig. 1. Images of fungi growing and interacting in agar media. Panel A shows a range of fungi used in pairwise competitive interactions. Panel B shows fungi that have been growing at a range of different temperatures that are used to reflect an environmental gradient. Panel C shows three interacting cultures of the same fungal isolate.

The recent shift towards natural substrates in experimental studies can certainly increase the strength of real world inferences. However, we suggest that the indiscriminate loss of ArtMed experiments might come at the expense of various mechanistic insights that can only be detected in such model systems, and this might place fungal ecology at a conceptual disadvantage compared to other fields of ecology. Despite a growing appreciation for the need to maintain more traditional, reductionist experimental research in light of emerging technological advances (Peay, 2014; Vilanova and Porcar, 2016), the use of ArtMed in experimental systems continues to fall. We believe that this stems partially from confusion over the appropriate use of ArtMed experimental systems. In this manuscript, we examine the pros and cons of using ArtMed in experimental fungal ecology, and we outline the types of questions that can effectively be addressed using ArtMed. We hope that this manuscript can provide a framework for the effective use of ArtMed in experimental fungal ecology.

2. Pros and cons of artificial media

The major criticism of artificial media conditions is their inability to replicate accurately natural conditions. Most artificial media provide homogeneous, well-mixed conditions that inherently fail to imitate the structural or chemical heterogeneity of most natural resources. As a result, the growth, morphology or biochemical activity of fungal isolates on agar is often drastically different from that on soil, litter or plant roots. Any inferences made about the foraging, population or community dynamics of fungi in natural systems based on experiments conducted solely in artificial media cannot be strong. For example, if fungus X displays a phalanx foraging strategy when growing on agar, we cannot make strong inferences about the foraging or competitive dynamics of that fungus under any particular set of natural conditions (Magan and Lacey, 1984; Boddy, 1993). Second, liquid ArtMed generally provide homogenous, well-mixed, non-solid environmental conditions, and solid ArtMed typically present relatively uniform growing conditions at the centimeter scale. Homogeneous conditions are unrealistic in many microbial systems (e.g., soil or root-associated fungi), which exhibit high spatial heterogeneity at the millimeter or micrometer scale.

Although these criticisms certainly limit the application or scaling of results from artificial media to the real world, they do not limit their utility in all aspects of fungal ecology. Despite the limitations regarding structural realism, they can certainly capture certain aspects of fungal dynamics that cannot be isolated in natural complex systems. ArtMed provide unrivalled simplicity, and they are unique in their capacity to use, manipulate and replicate. The transparent nature of many ArtMed allows them to provide a unique window into the activity of otherwise concealed individuals. Finally, they can be manipulated to approximate ‘optimal’ growing conditions for the determination of ‘potential’ activity, in the absence of exogenous factors. Below we outline the types of ecological question that lend themselves to the use of ArtMed in fungal ecology.

3. Appropriate use of artificial media in fungal ecology

A possible factor contributing to the decline in ArtMed is the