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Commentary

Lives within lives: Hidden fungal biodiversity and the importance of conservation

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ABSTRACT

Nothing is sterile. Insects, plants, and fungi, highly speciose groups of organisms, conceal a vast fungal biodiversity. An approximation of the total number of fungal species on Earth remains an elusive goal, but estimates should include fungal species hidden in associations with other organisms. Some specific roles have been discovered for the fungi hidden within other life forms, including contributions to nutrition, detoxification of foodstuffs, and production of volatile organic compounds. Fungi rely on associates for dispersal to fresh habitats and, under some conditions, provide them with competitive advantages. New methods are available to discover microscopic fungi that previously have been overlooked. In fungal conservation efforts, it is essential not only to discover hidden fungi but also to determine if they are rare or actually endangered.

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1. Introduction

As heterotrophs, fungi are essential to the functioning of terrestrial ecosystems (Taylor and Osborn, 1996; Moore et al., 2011), and they form symbiotic associations with all groups of organisms (de Bary, 1879). For example, almost all plants contain fungal endophytes within their leaves, stems, and roots (Redlin and Carris, 1996; Schulz et al., 2006; Pirttilä and Frank, 2011; Mayerhofer et al., 2013), and fungal endophytes may arm their associates with competitive advantages (Cheplick and Faeth, 2009; White and Torres, 2009; Vega, 2018). Also, all groups of fungi have evolved mycoparasitic life histories independently on many occasions (see below), and 80% of land plant species are presumably associated with mycorrhizal fungi (van der Heijden et al., 2015; Watkinson et al., 2016). Some insects rely on gut microbes to enrich the nutrient content and digestibility of their often-limited diets, and many fungi rely on insects for dispersal (Buchner, 1953, 1965; Vega and Dowd, 2005; Urubschurov and Janczyk, 2011; Douglas, 2015). Bacteria are increasingly being linked to associations with fungi and other organisms, and they may provide hosts with advantages over fungi because they fix nitrogen; fungi, however, synthesize sterols that are required by some of their associates, something that bacteria cannot do (Gibson and Hunter, 2010; Douglas, 2015; Blackwell, 2017a; 2017b).

The purpose of this commentary is to call attention to the fungal diversity hidden in associations with the highly speciose groups, plants, other fungi and insects (Vega and Blackwell, 2005; Watkinson et al., 2016), and to highlight the need to consider fungal genetic diversity when conservation decisions are made.

Despite multi-trophic level associations of fungi with bacteria and viruses in nature, they are mentioned only occasionally in this review. Because many fungal associates are microscopic, they are difficult to detect, and special effort is required to discover their presence.

2. Fungal diversity

Estimates of microbial diversity on Earth vary greatly, but since the development of methods to survey environmental DNA, the

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anticipated numbers have increased greatly, sometimes by several orders of magnitude. There are estimates of microbial numbers of all organisms on Earth that run as high as one trillion species, including bacteria, Archaea, and microscopic fungi (Locey and Lennon, 2016). Mycologists have been interested in fungal species diversity for several decades (Hawksworth, 1991, 2001; Hawksworth and Rossman, 1997; Blackwell, 2011; Hawksworth and Lücking, 2017) in order to understand better the effect of fungi on Earth and to justify their study (Hibbett et al., 2016). The number of fungi currently described is about 120,000 species (Hawksworth and Lücking, 2017). An estimate of the total number of undescribed fungi is more difficult to assess, and these estimates have varied depending on the methods used to collect and analyze them. Several estimates of total fungal numbers based on DNA data and extrapolation of fungi to plant ratios range from 3.5 to 5.1 (O'Brien et al., 2005) and 6 million species (Taylor et al., 2014). A more recent evaluation by Hawksworth and Lücking (2017) gave a lowered conservative estimate of 2.2–3.8 million species, based in part on new information of numbers of plant and insect species and their potential fungal associates. Based on these estimates, it is clear that “over 90% of fungal diversity on Earth remains to be discovered” (Tripp et al., 2017). See below (*2.2. Hidden fungal biodiversity: Fungi associated with insects*) for a continuation of this topic in connection with numbers of insects.

Studies involving fungal biodiversity and genes responsible for a distinctive biological process should be as important as research focused on functional-trait ecology (Crowther et al., 2014), which tries to elucidate the role of an organism on the community: “Looking at species number alone … is like listing the parts of a car without saying what they do” (Cernansky, 2017). Not only are there a plethora of fungi to be discovered, but their role in ecological processes remains to be determined. Gradually, information on the contributions of fungi is being discovered. For example, Taylor et al. (2014) tied ecological observations to their accompanying phylogenetic analyses showing a pattern interpreted as niche partitioning in community assembly based on the divergent niches of closely related taxa in the ecologically and taxonomically diverse soil fungi they identified.

2.1. Hidden fungal biodiversity: Fungi associated with plants

Symptomless leaf, stem, and root endophytes are numerous (Petrini, 1991; Hyde and Soytong, 2008). Smith et al. (2008) referred to fungal and bacterial endophytes when they stated, “Each of the nearly 300,000 species of land plant on Earth is likely to host one or more endophyte species.” Based on the large majority of existing fungal endophyte surveys, this is very likely an underestimation of fungal endophyte presence. Several studies have reported on the large fungal biodiversity in plants: 418 morphospecies, equivalent to ca. 347 distinct taxa, in *Heisteria concinna* and *Ouratea lucens* (Arnold et al., 2000); 344 morphotaxa in *Theobroma cacao* (Arnold et al., 2003); 257 unique ITS genotypes in *Coffea arabica* (Vega et al., 2010); 196 species in *Arctostaphylos uva-ursi* (Widler and Müller, 1984); 155 species in *Carpinus caroliniana* (Bills and Polishook, 1991); and 149 species in *Quercus ilex* (Collado et al., 1999).

Surveys of fungal stem and leaf endophytes have resulted in the discovery of new ascomycete species: *Penicillium coffeae* in *C. arabica* (Peterson et al., 2005); *Muscodor yucatanensis* in *Bursera simaruba* (González et al., 2009); Mycosphaerella sp. nov. in *Psychotria horizontalis*, with metabolites that include cercosporins with high potency against the causal agents of malaria, leishmaniasis, and Chagas disease (Moreno et al., 2011); and *Kabatiella bupleuri* in *Bupleurum gibraltarium* (Bills et al., 2012a). In a few cases, fungi in lineages known previously as insect associates and wood decayers, are also being discovered to have a life as endophytes (Martin et al., 2015; Baral et al., 2018).

Even though many papers have reported the presence of fungal endophytes in roots (Stone et al., 2004; Schulz et al., 2006), these are not as well characterized as other root-associated fungi such as facultative biotrophic ectomyorrhiza or obligate biotrophic arbuscular mycorrhiza. According to Zuccaro et al. (2014), “There is growing evidence that root endophytic associations, which due to their inconspicuous nature have been often overlooked, can be of mutualistic nature and represent important players in natural and managed environments.” Fungal endophytism in the root is therefore an area that should be studied in earnest, not only because it might reveal new fungal species among other hidden fungal diversity, but also because these fungi might play an important role in the biology of the plant.

As was noted above, 80% of land plant species are presumably associated with mycorrhizal fungi. Ectomycorrhizas constitute the most species diverse group with 20,000 species including representatives of 16 orders of Basidiomycota, Ascomycota, and Endogonales (Tedersoo et al., 2010; van der Heijden et al., 2015). Arbuscular mycorrhizas (AM fungi) may be associated with up to 74% of all plant species (200,000 species) but are probably underestimated as numbering fewer than 2000 species (Wang and Qiu, 2006; van der Heijden et al., 2015). Accumulating evidence indicates that AM fungi are more species diverse than previously acknowledged, due in part to species delimitation based on few morphological characters (Bruns and Taylor, 2016; Savary et al., 2018). Other specialized mycorrhizal groups include those associated with ericoids and orchids. DNA studies indicate that the species rich Orchidaceae have rather specific fungal associates (Otero et al., 2002; Taylor et al., 2002).

2.1.1. Examples of interactions among fungi and plants

Numerous potentially useful compounds have been discovered in endophytes and endolichenic fungi and have encouraged searches for new medicines in the pharmaceutical industry. The fungi often play a protective or other interactive role in their hosts, and the associations between endophyte and host can be important in searches for bioactive compounds (Paranagama et al., 2007; Kannangara et al., 2009; Kusari et al., 2012; Card et al., 2016). The identification of *Neotyphodium coenophialum*, the agent of “fescue toxicosis” in cattle consuming infected strains of *Festuca arundinacea* 50 y ago was a landmark in the study of fungal secondary metabolites (Bacon et al., 1977).

Fungi produce secondary metabolites that can have adverse effects on other fungi, mammals, including humans (e.g., mycotoxins), and plants (e.g., phytotoxins). Some of the metabolites have important medicinal properties (e.g., cephalosphorins, cyclosporins, penicillins), and others are used in the agrochemical (e.g., fumagillin, gibberellic acid) and cosmetics industry (e.g., kojic acid) (Bills and Gloer, 2016). One of the first examples of drug discovery involving a fungal endophyte was the antifungal drugs produced by various strains of *Cryptosporiopsis* isolated from plant roots (Tscherter and Dreyfuss, 1982). Some endophytes are known to have antiviral activity, e.g., inhibitors of human cytomegalovirus protease and HIV-1 division replication, activity against cancer, tuberculosis, fungi, and malaria; and control of cholesterol levels (Prakash, 2015).

In some cases, the search for potential drugs, including from endophytes, has been guided by traditional uses suspected long ago (Gordien et al., 2010). Not all researchers are convinced that the use of endophytes has paid off for commercial production of pharmaceuticals, although they offer suggestions to promote greater success (Kusari et al., 2014; Card et al., 2016). Newly developed techniques, including use of genomics, could be useful in making

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