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## Review

# Lineages of ectomycorrhizal fungi revisited: Foraging strategies and novel lineages revealed by sequences from belowground<sup>☆</sup>



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### ABSTRACT

In the fungal kingdom, the ectomycorrhizal (EcM) symbiosis has evolved independently in multiple groups that are referred to as lineages. A growing number of molecular studies in the fields of mycology, ecology, soil science, and microbiology generate vast amounts of sequence data from fungi in their natural habitats, particularly from soil and roots. However, as the number and diversity of sequences has increased, it has become increasingly difficult to accurately identify the fungal species in these samples and to determine their trophic modes. In particular, there has been significant controversy regarding which fungal groups form ectomycorrhizas, the morphological “exploration types” that these fungi form on roots, and the ecological strategies that they use to obtain nutrients. To address this problem, we have synthesized the phylogenetic and taxonomic breadth of EcM fungi by using the wealth of accumulated sequence data. We also compile available information about exploration types of 143 genera of EcM fungi (including 67 new reports) that can be tentatively used to help infer the ecological strategies of different fungal groups. Phylogenetic analyses of ribosomal DNA ITS and LSU sequences enabled us to recognize 20 novel lineages of EcM fungi. Most of these are rare and have a limited distribution. Five new lineages occur exclusively in tropical and subtropical habitats. Altogether 46 fungal genera were added to the list of EcM fungal taxa and we anticipate that this number will continue to grow rapidly as taxonomic works segregate species-rich genera into smaller, monophyletic units. Three genera were removed from the list of EcM groups due to refined taxonomic and phylogenetic information. In all, we suggest that EcM symbiosis has arisen independently in 78–82 fungal lineages that comprise 251–256 genera. The EcM fungal diversity of tropical and southern temperate ecosystems remains significantly understudied and we expect that these regions are most likely to reveal additional EcM taxa.

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## 1. Introduction

The ectomycorrhizal (EcM) symbiosis has evolved multiple times both in plants and fungi. The fungal kingdom includes at least 66 independent lineages of EcM fungi, mostly members of the Basidiomycota and Ascomycota (Tedersoo et al., 2010). In the past it has been challenging to unambiguously determine whether some fungal groups are ectomycorrhizal or not because of limited or ambiguous evidence and alternative interpretations (Rinaldi et al., 2008; Tedersoo et al., 2010; Comandini et al., 2012; Ryberg and Matheny, 2012). However, community studies of ectomycorrhizal fungi have become more sophisticated over the past two decades and a variety of techniques have been used to determine EcM status and to delimit groups of EcM taxa, including experimental synthesis trials, field observations combining anatomical and molecular techniques, stable nitrogen and carbon isotope signatures, and phylogenetic analyses. Unfortunately, many EcM fungal taxa detected as environmental sequences do not match sequences of fruit-body vouchers or pure cultures (Tedersoo et al., 2010). Although reference sequences from fruit-bodies are accumulating at an exponential rate, many sequences from EcM root tips remain unmatched to their sexual stages. This suggests that much of the EcM fungal diversity is indeed cryptic. Nevertheless, many described species and even genera lack publicly available sequence data (Tedersoo et al., 2010) and this underscores the need to produce DNA sequences from identified herbarium specimens (Brock et al., 2009).

The rapidly growing DNA sequence data in public repositories, in conjunction with recently developed sequence annotation tools (e.g. PlutoF workbench – Abarenkov et al., 2010; Tedersoo et al., 2011a), provide an invaluable source of metadata about the host plants, isolation sources, and geographic origin of EcM fungal isolates. By using the data in public sequence databases, Hynson et al. (2013), Tedersoo et al. (2013a) and Veldre et al. (2013) recently detected additional putative EcM lineages within the Serendipitaceae (Sebacinales group B), Pyronemataceae and Ceratobasidiaceae. These fungal lineages were previously considered root endophytes, saprotrophs or parasites. The limited number of sequences from these lineages suggests that they are uncommon in EcM fungal communities or were considered root contaminants in the original studies (e.g. Oberwinkler et al., 2013).

It is important to understand which fungal taxa are EcM and which are not. EcM fungi play fundamentally different roles in forest communities and in ecosystems compared to other functional guilds such as fungal root endophytes and decomposers. For example, EcM fungi are uniquely adapted to facilitate mineral nutrition of plants and to distribute recent photosynthates into the mycorrhizosphere soil (Buee et al., 2009). Mycorrhizal fungi have mostly lost the powerful enzymes used for attacking plant cell walls and degrading organic compounds such as lignin (Eastwood et al., 2011). Furthermore, since EcM fungi are often the most abundant organisms in forest soils, it is important to understand their ecology for the purposes of management and conservation. This is particularly relevant for taxa in the Ceratobasidiaceae, since this group includes beneficial orchid and

ectomycorrhizal symbionts as well as devastating fungal plant pathogens (Veldre et al., 2013). Several lineages within Pezizales are associated with tree roots in truffières where they compete for space and resources with the valuable truffle “crop” species (Bonito et al., 2011, 2012; Rubini et al., 2011). However, most species of Pezizales are saprotrophic and a few are pathogenic (Hansen and Pfister, 2006). The rapid shift from root tip-based studies to soil fungal community studies necessitates discriminating between mycorrhizal and non-mycorrhizal fungi. Molecular studies of soil increasingly use sophisticated second and third generation sequencing technologies to generate millions of reads. In contrast to EcM roots and fruit-bodies that can be stored as vouchers and morphologically examined in the future, soil-based studies cannot provide morphological or ultrastructural information to infer ecological interactions. These high-throughput sequencing methods are an easy and cost-effective way to study mycorrhizal ecology in situ but currently our ability to adequately identify fungal DNA sequences and interpret the ecological role of these species is lagging behind our ability to produce sequence data. The phylogenetic and functional breadth of fungi in soil and other complex substrates poses a great challenge for taxonomic identification as well as functional characterization. Because of the large volume of sequence data and the large number of fungal taxa involved in the EcM symbiosis, researchers would benefit from a well-annotated reference database from which they can automatically extract information on ecology and taxonomy of fungal taxa (Köljalg et al., 2013).

Within EcM fungi, there are major differences in ecological strategies of dispersal (Ishida et al., 2008), metabolic activity (Trocha et al., 2010) and in relative benefits to plant hosts (van der Heijden and Kuyper, 2003; Nara, 2006). This is at least partly ascribed to differences in the relative carbon cost to plants and efficiency in enzymatic access to organically bound nutrients, nutrient uptake and nutrient transfer (Courty et al., 2010). Species of EcM fungi differ strongly in their potential enzymatic capacity, which is a function of both the substrate and climatic conditions (Courty et al., 2010). Evidence suggests that key enzyme functions are highly variable between (and within) EcM lineages and are partly predictable based on phylogenetic relationships among the EcM fungi (Tedersoo et al., 2012b). Not surprisingly, the abundance and morphology of the extraradical mycelial system is the single most important variable in determining enzymatic capacity (Tedersoo et al., 2012b). The presence and characteristics of extraradical hyphae and rhizomorphs serve as proxies for foraging strategies referred to as “exploration types” (Agerer, 2001, 2006). Species of medium-distance and long-distance exploration types tend to exhibit similar responses to climatic gradients (Ostonen et al., 2011), N fertilization or pollution (Lilleskov et al., 2011; Kjoller et al., 2012) and carbon influx (Markkola et al., 2004). Most fungi with long-distance exploration strategies appear specialized in N uptake from organic sources and they apparently expend significant carbon resources on rhizomorphs so they appear to lose their relative benefits or competitive abilities in disturbed systems (Lilleskov et al., 2011). In contrast, smooth and short-distance exploration types are more frequently detected in

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