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**Key words:** demographic limits, dispersal, genetic constraints, mating system, range expansion.

## Letters

## Ectomycorrhizal fungi and the biotrophy–saprotrophy continuum

Frank (1885, English translation 2005) studied the associations between members of the Pinaceae, Salicaceae, Corylaceae and Fagaceae and certain fungi that envelop their feeder rootlets. He speculated that these 'mycorrhizas', as he called them, particularly those involving the Corylaceae and Fagaceae,

were mutualistic associations. Some have since come to define all mycorrhizas as mutualistic associations (Harley & Smith, 1983; Allen, 1991). Others (Johnson *et al.*, 1997; Jones & Smith, 2004) have discussed the evidence that mycorrhizal fungi can actually be either mutualistic or parasitic with respect to their hosts, depending on the conditions, and we do not intend to revisit that issue here. By way of introduction to the topic at hand, however, we point out that mutualism and parasitism result from the nature of bidirectional resource transfers. For example, mutualism results from the net transfer of resources that limit the host (such as phosphorus (P) or nitrogen (N)) from the fungus to the host, and the net transfer

of resources that limit the fungus (such as carbohydrate), from the host to the fungus.

In defining mycorrhizas, Trappe (1996) focused on the transfer of resources from the fungus to the host. Because the fungus ensheathed the entire rootlet, Frank (1885) reasoned that the fungus must first take up nutrients from the soil and then pass them along to the root. Colonization of roots by an ectomycorrhizal fungus, however, does not always result in increased nutrient absorption by the plant (Perez-Moreno & Read, 2000). Apparently the fungus is capable of acting independently from the host to the extent that it can withhold nutrients in its possession from the host. Indeed, nutrient immobilization by the fungus might be expected whenever the fungus cannot first satisfy its own nutrient requirements (Colpaert & Verstyuyt, 1999; Koide & Kabir, 2001).

The transfer of resources (particularly carbohydrate) from the host to the fungus constitutes biotrophy. The conventional view of ectomycorrhizal fungi is that they obtain reduced carbon exclusively or largely biotrophically (Read & Perez-Moreno, 2003; Jones & Smith, 2004). Owing to the intimate association between the fungus and the root, Frank (1885) reasoned that in the ectomycorrhizal associations he observed, the fungi did obtain carbon biotrophically. He further noted that 'true truffles occur only with living trees ...', and he described ectomycorrhizal fungi as 'parasitic' (Frank, English translation 2005), which we interpret today as 'biotrophic'. Since then, considerable evidence for biotrophy has accumulated. Rommell (1939) showed that many ectomycorrhizal fungi failed to fruit if isolated from living roots by trenching, and Högborg *et al.* (2001) demonstrated that girdling of host trees essentially eliminated fruiting of ectomycorrhizal fungi. Hutchison (1990), Colpaert & van Laere (1996) and Bending & Read (1997) demonstrated that many ectomycorrhizal fungi possess only marginal saprotrophic capacity compared with 'true saprotrophs'.

It is apparently a natural tendency for humans to place information into neat pigeonholes and, in this particular instance, two historical pigeonholes for fungi are the 'biotrophic' and 'saprotrophic' modes of nutrition. Hering (1982) proposed, for example, that decomposer and ectomycorrhizal fungi were to be found in 'two watertight, mutually exclusive classes'. The noted ecologist, H. A. Gleason, once warned 'As accumulation of knowledge continues, we eventually find facts that will not fit properly into any established pigeonhole. This should at once be the sign that possibly our original arrangement of pigeonholes was insufficient and should lead us to a careful examination of our accumulated data' (Gleason, 1926). There are undoubtedly species of ectomycorrhizal fungi that are entirely biotrophic and species of decomposer fungi that are entirely saprotrophic (Högborg *et al.*, 1999; Hobbie *et al.*, 2002). However, it now seems that there is ample justification for re-examining the 'original arrangement of pigeonholes' owing to the rapidly accumulating evidence of a range of trophic function among some ectomycorrhizal fungal species

(Dighton, 1991; Cairney & Burke, 1994; Colpaert & van Laere, 1996).

Indeed, Lewis (1973) recognized a problem in categorizing higher fungi on the basis of their trophic status when he acknowledged the possibility of facultative trophic forms. In the case of ectomycorrhizal fungi, facultative types are those that are capable of obtaining carbon both biotrophically and saprotrophically (Meyer, 1966). Evidence for the existence of facultative ectomycorrhizal fungi is now abundant. Saprotrophic capacity may be particularly well-developed among the pezizalean (Ascomycota) ectomycorrhizal fungi (Egger, 2006), but saprotrophy has also been described for many basidiomycotan ectomycorrhizal fungi (Lindeberg, 1948; Rawald, 1962; Lyr, 1963; Ritter, 1964; Ferry & Das, 1968; Palmer & Hacskeylo, 1970; Lamb, 1974; Trojanowski *et al.*, 1984; Dahm *et al.*, 1987; Erland *et al.*, 1990; Haselwandter *et al.*, 1990; Durall *et al.*, 1994; Tibbett *et al.*, 1998; Egger, 2006 and references therein). A range of trophic status is consistent with the observation that some fungi possess carbon signatures that are intermediate between those of purely biotrophic and purely saprotrophic fungi (Högborg *et al.*, 1999; Hobbie *et al.*, 2002). If biotrophy evolved from saprotrophy, as hypothesized (Hibbett *et al.*, 2000), it stands to reason that some ectomycorrhizal fungi would still possess saprotrophic capacity (Gramss *et al.*, 1998; Lindahl & Taylor, 2004; Egger, 2006; Courty *et al.*, 2007), particularly if there were some selection pressure maintaining it, such as the occasional loss of connection with a living host plant.

While there is as yet no evidence that an ectomycorrhizal fungus can complete its life cycle in the absence of a living host plant (Taylor & Alexander, 2005), the host may not be the only source, or even the main source, of energy for all ectomycorrhizal fungi, depending on host species, age, physiological status and environmental conditions. Therefore, we suggest that the distinction between biotrophic, ectomycorrhizal fungi and saprotrophic, decomposer fungi is artificial. We propose that ectomycorrhizal fungi can occur along a large portion of the biotrophy–saprotrophy continuum.

The arbitrary distinction between ectomycorrhizal fungi and decomposer fungi is further illustrated by the fact that some wood rotters actually form characteristic ectomycorrhizal structures, such as sheaths and Hartig nets with healthy roots (Pilz *et al.*, 2007; Vasiliauskas *et al.*, 2007), and some *Morchella* spp. may obtain a limited amount of carbon from the plant (Hobbie *et al.*, 2001). There are a number of reasons why this should not surprise us. First, decomposer fungi obtain carbon saprotrophically by colonizing litter, growing amongst the dead cells of leaves, stems and roots. The formation of a Hartig net among the living cells of a root would therefore not appear to be an unnatural process for decomposer fungi. Second, the distinction between obtaining carbon from living and dead plant tissue is somewhat arbitrary. Pure saprotrophs wait until the death of the tissue before colonizing it. In the

evolution of the ectomycorrhizal habit, some fungi may have positioned themselves among living cells of the roots in anticipation of their death before other saprotrophs could access them. It is, after all, the ectomycorrhizal fungus that has the first opportunity to act as a saprotroph once the root does die! The ectomycorrhizal habit could be considered as a special case of saprotrophy in which the food source is colonized before death, rather than after, and in which degradative enzyme production is largely attenuated during the living phase of the host (Colpaert & van Laere, 1996). Third, homobasidiomycetes and many Ascomycota regularly form pseudoparenchymatous tissues to produce fruiting bodies, so the formation of a root sheath by decomposer fungi would not represent any great problem of development. Finally, it would not be surprising to discover the transfer of P or N from a decomposer fungus to a plant root because the net movement of P or N into litter of a high C : P or C : N ratio appears to be a normal function among the litter-decomposing fungi (Berg & Ekbohm, 1983; Upadhyay & Singh, 1989; Gallardo & Merino, 1992; Koide & Shumway, 2000). Therefore, it would seem that in the evolution of ectomycorrhizal fungi from decomposer fungi there was not necessarily a single, fateful leap from pure saprotrophy to pure biotrophy but, in at least some cases, a series of incremental shifts along the continuum from saprotrophy towards biotrophy.

Because some ectomycorrhizal fungi possess significant saprotrophic capacity and some decomposer fungi form ectomycorrhiza-like structures, there does not appear to be any logical place to draw a line along the biotrophy–saprotrophy continuum to distinguish ectomycorrhizal fungi from decomposer fungi. Therefore, we suggest that placement along the biotrophy–saprotrophy continuum is useful in *describing* an ectomycorrhizal fungus in a particular symbiosis, but that the adjective 'biotrophic' cannot be used to *define* all ectomycorrhizal fungi any more than the description 'ten meters tall' can be used to define all trees.

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**Key words:** biotrophy, decomposer fungi, ectomycorrhizal fungi, mutualism, saprotrophy.

## Mycorrhizal status of native trees and shrubs from eastern Madagascar littoral forests with special emphasis on one new ectomycorrhizal endemic family, the Asteropeiaceae

Mycorrhizas are ecologically important symbioses in which the fungi derive photosynthetic sugars from their plant hosts, which in turn benefit from fungus-mediated uptake of mineral nutrients. Depending on the relative arrangements of the fungus and the root, mycorrhizal symbioses have been classified into two major types: endomycorrhizas and ectomycorrhizas (ECM). Within endomycorrhizas, arbuscular mycorrhizas (AM) are presumed to have been crucial in the colonization of the land by plants (Pirozynski & Malloch, 1975; Selosse & Le Tacon, 1995; Taylor *et al.*, 1995; Heckman *et al.*, 2001); evolutionary studies based on fossil evidence (Simon *et al.*, 1993; Redecker *et al.*, 2000) and molecular clock estimations (Berbee & Taylor, 2001) have shown the ancestral character of this symbiosis (Fitter & Moyersoen, 1996; Cairney, 2000; Wilkinson, 2001), in which a broad range of herbaceous and woody plants are associated with a fungal phylum: the Glomeromycota (Sch   ler *et al.*, 2001). The other important group of mycorrhizas are ECM, in which mainly Homobasidiomycetes are associated with about 20 families of mainly woody plants (Brundrett, 2002).

Madagascan forests are characterized by high botanical diversity with a high degree of endemism in the vascular plant flora, estimated at 80% (Lowry *et al.*, 1997). They also have one of the highest concentrations of endemic plant families in the world: eight families represented by a total of 17 genera totalling *c.* 90 species (Schatz *et al.*, 1999). The occurrence and types of root symbiosis are poorly known in the Madagascan