

Commentary

The danger of mycorrhizal traps?

Conventional wisdom considers the mycorrhizal symbiosis as mutualistic because both the mycorrhizal fungus and the mycorrhizal plant potentially benefit from the exchange of nutrients and carbon (C). Cases in which mycorrhizal plants are smaller than nonmycorrhizal plants have been reported (Klironomos, 2003). While these cases are often considered exceptions, they raise an important question of partner control. How do plant and fungal partners ensure that they are getting a 'fair-deal' for the resources they are trading, and avoid being cheated (Ghoul *et al.*, 2014)? Does engaging in a mutualistic partnership translate into consistent and measurable benefits? Recently, Näsholm *et al.* (2013) explicitly addressed the question of whether ectomycorrhizal fungi alleviate or aggravate nitrogen (N) limitation of conifers in boreal forests. They concluded that, in these systems, ectomycorrhizal fungi immobilize large quantities of N and thus drive N limitation for host plants. In this issue of *New Phytologist*, Franklin *et al.* (pp. 657–666) expand upon that hypothesis. In their paper they provide a model that predicts that trees associating with ectomycorrhizal fungi show reduced performance. The work explores the idea of how trees can become 'trapped' by these dynamics, unable to eliminate their mycorrhizal fungal partners under conditions where a nonmycorrhizal habit would be more beneficial, even if this appears to be 'maladaptive'.

'How do plant and fungal partners ensure that they are getting a "fair-deal" for the resources they are trading?'

The Franklin *et al.* model is interesting because it examines the mutualism from an economic vantage point (Werner *et al.*, 2014), asking how competition between partners affects trade dynamics. For a market mechanism to be invoked, there must be multiple partners on both sides of the mutualism offering different prices or services (Noë & Hammerstein, 1995; Kiers *et al.*, 2011; Fellbaum *et al.*, 2014). In the ectomycorrhizal mutualism, one fungal individual can be simultaneously connected with different individual trees (potentially offering different amounts of C), and individual trees are usually colonized by more than one fungal individual (potentially offering different amounts of various nutrients). While market models have been used in the past to explore mycorrhizal dynamics (Hoeksema & Schwartz, 2001, 2003; Kummel & Salant, 2006; Grman *et al.*, 2012), this model is different because it is parameterized using field-scale dual N and C

isotope labelling experiments. This allows for a level of realism and predictive accuracy not found in many other models.

The model is also elegant in that it is captured by a few crucial elements, namely established equations for N-limited plant growth and C-limited (or C and N co-limited) fungal growth. While the underlying mathematical structure is seemingly complex, the model is phrased in nonmathematical terms and all the maths are relegated to supplementary material. Importantly, the model allows for strategies of individuals to adapt to both the biotic and abiotic environment via maximizing fitness equations. Both trees and fungi have the potential to increase their fitness by achieving a more favourable C-for-nutrient trade than their competitors.

Franklin *et al.* use their model to predict the conditions leading to invasibility by a nontrading partner (in this case situations in which nonmycorrhizal trees can outcompete mycorrhizal trees). They find that, under N limitation, a nonmycorrhizal tree cannot invade, a situation that ultimately fosters the initial brokering of the deal between hosts and the mycorrhizal fungi, which can be later difficult to terminate. At the other side of the spectrum, under N enrichment, the model predicts a rapid switch from a mycorrhizal to a (partly) nonmycorrhizal condition. Physiologically, however, a rapid strategy switch to a nonmycorrhizal condition may be impossible – the host is potentially 'trapped' into a binding agreement, even though the terms of trade have shifted as N becomes more available. Their model is nicely summarized in their Fig. 6, showing that under N limitation increased C allocation by the tree feeds back into increased N uptake by the fungus (and increased N immobilization by fungal biomass), which further depletes soil N and increases tree dependence on the interaction. This type of dynamic is reminiscent of other evolved dependencies, such as the dependency of the blight fungus *Rhizopus* on the presence of endobacteria (*Burkholderia* sp.) for its reproduction (Partida-Martinez *et al.*, 2007); while initially such partnerships may have had a selective advantage, such dependencies can eventually be harmful to the host if, ultimately, they are unable to rid themselves of the costly microbial interaction (Ellers *et al.*, 2012; Werner *et al.*, 2014).

Their work has a number of relevant implications. While decline of ectomycorrhizal fungi under N enrichment has already been demonstrated in a multitude of studies, their model also predicts (1) the existence of two stability regimes of ectomycorrhizal symbioses (namely, mycorrhizal with a rapid switch to a partly nonmycorrhizal condition driven by N enrichment) and (2) a strong coupling between N retention and ectomycorrhizal fungi, which allows for legacy effects (i.e. a dependence both on current input and historical inputs) if forests recover from N saturation (Högberg *et al.*, 2011). The model furthermore suggests that under increasing atmospheric CO₂ concentrations, the ectomycorrhizal symbiosis could further aggravate N limitation, which then prevents trees from benefitting from increased CO₂

concentrations. Several published studies are in agreement with this hypothesis, which was earlier phrased as 'progressive nitrogen limitation' (Alberton *et al.*, 2007).

The paper also raises a number of points for future studies. A major question is about the generality of their model. Does it apply exclusively to ectomycorrhizal systems or would the model predict similar outcomes for the arbuscular mycorrhizal (AM) symbiosis? For example, the more open N cycle in AM forests (Phillips *et al.*, 2013) is consistent with a hypothesis that the nutrient depletion feedback is less important in the AM symbiosis; the AM fungal biomass is thought to be one or two orders of magnitude smaller than ectomycorrhizal fungal biomass in the boreal forest. The open N cycle in tropical ectomycorrhizal forest (Tederloo *et al.*, 2012) potentially allows the Franklin *et al.* model to be tested in a different biome to tease apart these effects.

A further question refers to the symmetry of the model. Would a nonsymbiotic (i.e. a saprotrophic strategy) be possible for ectomycorrhizal fungi at high N availability? Saprotrophic behaviour of ectomycorrhizal fungi has been regularly proposed but strong empirical evidence is hitherto lacking. This potential asymmetry (in case the mycorrhizal fungi cannot revert to a free-living saprotrophic life style) in bargaining power has the potential to drive different selection dynamics. Several recent papers have suggested that ectomycorrhizal fungi play a role in N mining of soil organic matter (Bödeker *et al.*, 2014; Phillips *et al.*, 2014). This leads to a different role of the ectomycorrhizal symbiosis in mitigating the effects of elevated atmospheric CO₂ – not through enhanced plant performance but rather via increased C storage (Averill *et al.*, 2014).

Finally, market models raise important questions about the evolution of species interactions in mutualisms (Werner *et al.*, 2014). How does specialization of fungi and trees affect trade dynamics? Boreal forests tend to be dominated by ectomycorrhizal fungi (amongst others, members of the genera *Cortinarius*, *Tricholoma*, *Suillus* and *Rhizopogon*) that show high degrees of host selectivity. Sporocarps of fungi of these genera are characterized by high $\delta^{15}\text{N}$ values, and these high values have been taken to imply efficient N transfer to tree hosts (Taylor *et al.*, 2003). However, more research is needed to document absolute transfer of N (taking mycelial biomass into account). With these data, researchers can better link the functional traits of the ectomycorrhizal fungi (exploration type, hydrophobicity of the mantle, etc.) to plant host benefits of having multiple fungal partners. The mycorrhizal system can also be used to study specialization on particular resources. When does natural selection favour the trading of a diverse set of commodities vs the trade of very specialized resources? Will species entirely abandon acquiring a resource directly, and vice versa? The work by Franklin *et al.* is likely to stimulate future research into economic dynamics in nature.

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Key words: carbon (C), competition, market model, modelling, mutualistic partnership, mycorrhizal symbiosis, nitrogen (N) limitation, trade.

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