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The mycorrhizal tragedy of the commons

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Ectomycorrhizal fungi (EMF) play a key role in the cycling of nitrogen (N) and carbon (C) in boreal forests. Trees receive growth-limiting N in exchange for allocating C to their mycorrhizal symbionts, but supplying the fungi with C can also cause N immobilization, which hampers tree growth. We present results from field and greenhouse experiments combined with mathematical modelling, showing that these are not conflicting outcomes.

Under N limitation, which is the general case in boreal forests, the plant host has been observed to continue supplying its ectomycorrhizal partner with C, and even increasing this C investment, while the fungus reduces mobilization of N to its host (Corrêa et al. 2008, 2010). N is thus withheld under conditions of limiting availability, and the host tree cannot unlock it by supplying the EMF with more C, because such an investment results in further diminishing N returns. Critical to this question is the observation that more than one fungus can form mycorrhiza on a given tree and that several trees can be connected to a given fungal individual (Southworth et al. 2005).

We hypothesize that plants sharing common ectomycorrhizal symbionts compete with each other for N by exporting C to the EMF network, and vice versa for a fungus. The fungi making up the EMF network export N to hosts if it is absorbed in excess of their own growth demand, which is limited by C; Exporting more than this would reduce their growth, exporting less would reduce their competitiveness for plant C (Näsholm 2013, Franklin 2014). This hypothesis has specific and predictable implications for relationship between plant C export to EMF and N uptake: At the community level, increasing plant C supply to EMF would increase both fungal N uptake and N use, but as soil N availability gradually becomes limiting, uptake should saturate while EMF N use continued to increase, leading to declining N export to plants.

We conducted two experiments, one in potted mesocosms and the other in a boreal forest setting. Belowground C flux was reduced by shading and/or stem strangling, which is a treatment whereby the flow of C to the root system is physically restricted by blocking transport through the phloem in the stem (Björkman 1944; Henriksson et al. 2015). Strangling a subset of seedlings growing in the same pot accomplishes two things: 1) the total belowground C flux is decreased, and 2) each

seedling's relative contribution to that flux is altered.

Based on measurements and mathematical modelling, we conclude that belowground C allocation by trees can indeed fuel N immobilization, reducing the amount of N to be distributed among the trees. But we also found that individual trees received nutritional benefits in proportion to their C contribution to the fungal network. We illustrate the evolutionary underpinnings of this situation by drawing on the analogous tragedy of the commons (Hardin 1968), where the shared mycorrhizal network is the commons, and explain how rising atmospheric CO_2 may lead to greater nitrogen immobilization in the future.