



Commentary

Uncommon ectomycorrhizal networks: richness and distribution of *Alnus*-associating ectomycorrhizal fungal communities

The level of specificity is a key evolutionary and ecological parameter of any symbiotic interaction. Where diverse classes of mutualists interact, extracting the drivers of spatial–temporal variation in community composition is also fundamental to understanding the interaction. Ectomycorrhizal (EM) plants and fungi typically associate with many symbionts both as individuals and across a species' range. Trappe (1977) estimated that *Pseudotsuga menziesii* is compatible with some 2000 species of EM fungi, an impressively high number that has stood the test of time but could be revisited. At the low end among autotrophic plants is the genus *Alnus*. Although it is known that the EM fungi associated with *Alnus* are not a rich community (Molina *et al.*, 1992), there is still debate about the factors that might drive this phenomenon, as well as its implications. In this issue of *New Phytologist*, two contributions on *Alnus* EM fungi help to fill this gap. Roy *et al.* (pp. 1228–1238) provide a detailed investigation of the fungal diversity of *Alnus* associates at a regional scale, while Pölme *et al.* (pp. 1239–1249) assess fungal biogeography at a global scale. Both studies carefully evaluate the influences of host phylogeny, geographic distance, climate and other environmental variables on patterns of plant–fungus association. We have entered a new era of molecular ecology research in which advanced molecular tools for documentation of microbial diversity and genetic variation are increasingly combined with sophisticated statistical tools of population genetics, phylogenetics and community ecology to provide deeper insights with rigorous scientific support. The simultaneous publication of two studies using the full range of these tools focusing on the same model system at two spatial scales exemplifies this trend, together providing important new insight into host and habitat factors driving host specificity and community dynamics.

Roy *et al.* sampled 165 trees belonging to five species in France and Corsica. Pölme *et al.* include root samples of 22 *Alnus* species collected from 96 stands across the broad geographic range of the genus. Surprisingly, this substantial difference in sampling scale yielded only a modest difference in EM fungal richness. Roy *et al.* report 86 molecular operational taxonomic units (MOTUs) from 1178 sequences in France and Corsica, while Pölme *et al.* report 146 MOTUs from 1172 sequences across the globe.

One of the important questions in EM ecology is what drives the composition and species richness of EM fungi found in plant communities (Bruns, 1995). The genus *Alnus*, with its low richness of EM fungi, provides an excellent model system to address this question. Pölme *et al.* found host species' phylogenetic relatedness had the greatest impact on EM fungal community composition, suggesting fungus-to-plant specificity at the subgeneric level. The second most important factor driving EM community composition was biogeography. The fungal communities recovered from northwest America shared the most MOTUs with those from Asia, while those from northeast America shared the most MOTUs with those from South America. The biogeographic patterns are not particularly well supported, but are not unique to *Alnus* fungi: the authors suggest they reflect host migration after the last glacial maximum. Surprisingly, higher richness at the global scale was correlated with increasing soil calcium (Ca) concentration, highlighting the need for additional research focused on mycorrhizal interactions and Ca biogeochemistry.

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Roy *et al.* found that richness (alpha diversity) was significantly influenced by soil (mineral vs organic) but not host species or subgenus. Unlike Pölme *et al.*, these authors did not detect an influence of Ca concentration on EM fungal diversity, while soil organic matter, carbon (C), nitrogen (N), phosphorus (P) and potassium (K) all influenced fungal community composition across sites (beta diversity). These soil parameters in combination with host explained 26% of the variation of the community structure in the *Alnus* stands sampled. While altitude may have shaped the communities, the authors could not rule out the role of host specificity at the subgenus level. Host, soil parameters, altitude and longitude all influenced community similarity.

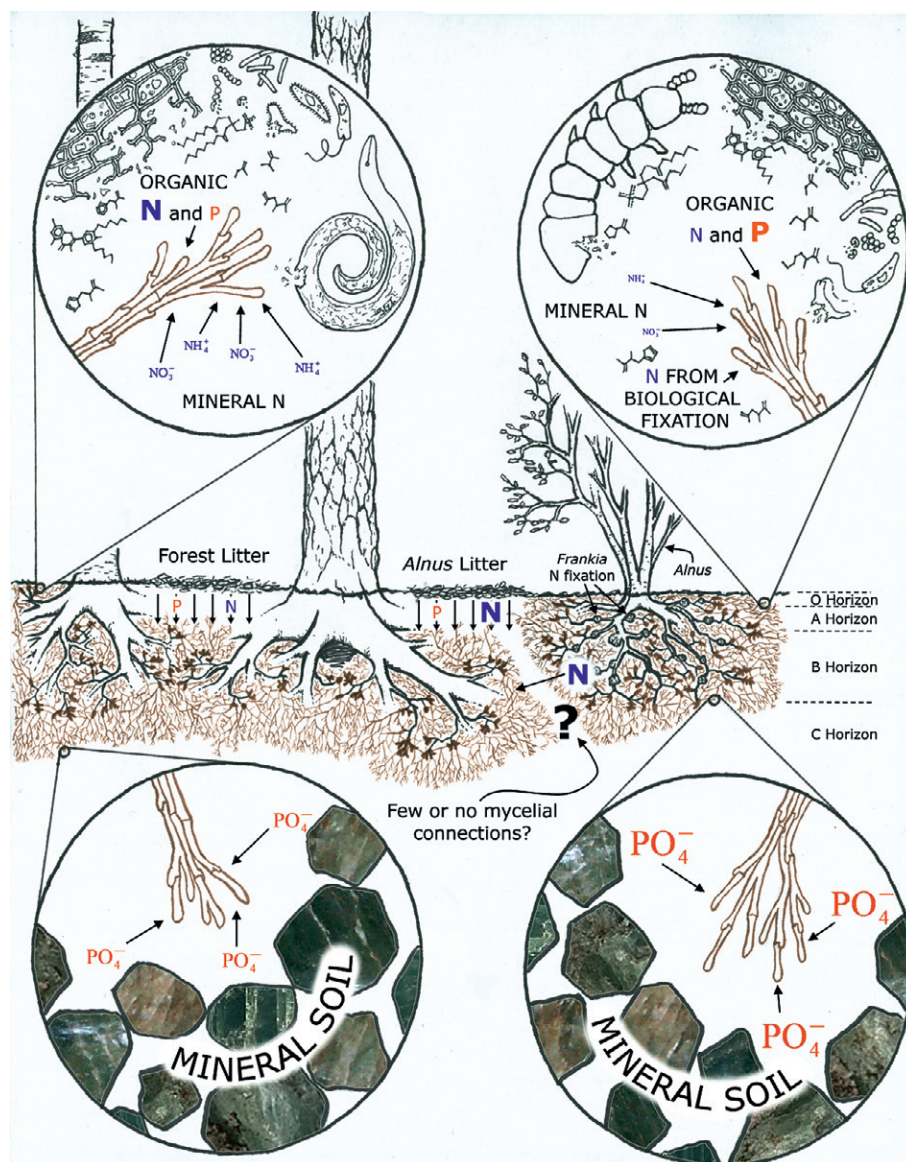
It is worth mentioning that the most frequently encountered fungi showed the lowest specificity in these studies. This pattern is predicted for mutualistic networks, and has been found in numerous symbioses, including mycorrhizas (Bascompte & Jordano, 2007; Martos *et al.*, 2012). Perhaps this is a sampling issue in this case – the chance of not encountering a fungus–host pairing is greatest for uncommon fungi. But it is also interesting to speculate whether the frequency of common fungi is caused by

their low specificity: are they frequent because associating with a greater number of hosts facilitates their establishment? Along these lines, Vanderplank (1978) suggested that resistance to a mutualist must reduce fitness, because mutualists (by definition) enhance fitness. But then, why are some fungi narrowly host-specific at the genus or even subgenus level, like *Naucoria* spp. are with *Alnus* or *Alboalnus*?

Perhaps the specificity is related to the nutrient needs and physiology of the symbionts (see Fig. 1). No conclusive link between engaging in an N-fixing symbiosis (as *Alnus* does with the actinomycete *Frankia*) and EM specificity has been demonstrated. The coincidence of two unusual ecological features (N-fixation and specificity) invites speculation about a causal link. Much has been written about the evolutionary dynamics resulting in specificity in mutualisms (Thompson, 1994; Hoeksema, 1999). We speculate that *Alnus*' high P demand, in conjunction with a reduced need for fungus-derived N, provides selection pressure for the plant to

associate with fungi that are P specialists but may provide little N (Fig. 1). However, explaining the selective pressure for specialization on *Alnus* by the fungi is a major theoretical challenge. We must also keep in mind that other nutrients may be involved in these dynamics. For instance, Pölme *et al.* report strong community responses to Ca. The Ca effect might involve the survival or performance of fungi in soil, or might be mediated indirectly, that is, through *Alnus* ecophysiology and partner choice. However, if EM fungi protected plants from excess Ca, we would expect a lower richness of EM fungi with increased Ca. It has recently been shown that the same *Alnus* species associate with different *Frankia* across a strong local gradient in N and P forms and availability, and it has been suggested that these patterns arise from plant choice rather than direct effects on the bacteria (Anderson *et al.*, 2013). Clearly there is more work to be done on the mechanisms that drive specificity phenomena in mycorrhizal symbioses and we feel the science is primed to investigate the role of physiology.

Fig. 1 Conceptual schematic of ectomycorrhizal (EM) networks. Mycelial networks associated with EM hosts in mixed forests and *Alnus* are made of many species and individuals of EM fungi. The tree roots and fungi likely explore common zones in the soils. The question mark indicates that we are unclear how the species interact when they explore the same zones. *Frankia* derived nitrogen (N) is harvested from *Alnus* litter and root nodules by *Alnus* and forest EM fungi. However, the fungi apparently do not frequently form common mycorrhizal networks by colonizing both *Alnus* and forest tree roots. The hypothesized importance of nutrients to the organisms involved is shown by the size of the font. For example, bold, large font for phosphorus (P) and smaller font for N in the *Alnus* organic N and P window indicates our hypothesis that *Alnus*-associated fungi are important for the acquisition of P but less so for N and the dynamic is reversed in the forest organic N and P window. The schematic shows other hypotheses about the sources of N and P but it is not meant to be exhaustive. Indeed, we look forward to adding hypotheses about calcium dynamics to this schematic.



While both Roy *et al.* and Pölme *et al.* emphasize the importance of host identity in determining fungal community structure and richness, both studies also note significant spatial structure. Pölme *et al.* report broad-scale biogeographical trends which are largely congruent with historical plant host migrational patterns, although several MOTUs have unexpected intercontinental distributions. Roy *et al.* report little evidence for large-scale geographic structure in *Alnus* fungi across France and Corsica and emphasize the role of local-scale phenomena over geography in determining communities. Both studies report that several *Tomentella* MOTUs have broad ranges, while some other groups such as *Geopora* were much more limited in extent. As Pölme *et al.* point out, determining the extent to which limited ranges reflect dispersal abilities versus, for example, edaphic specialization, is difficult at this time. However, the substantial ranges of some MOTUs such as *Tomentella subulacina* OTU2, which Pölme *et al.* report from every region they sampled, strongly suggests that at least some fungi have undergone remarkable migrations. While ITS data alone do not reveal whether there is current gene flow between these disjunct populations, the colonization of several continents itself testifies to impressive dispersal abilities across geologic time, likely since the last glacial maximum (Vincenot *et al.*, 2012). The strong evidence for co-migration of *Alnus* and its fungi reported in both papers is important, again setting this interaction apart from most EM symbioses in which the linkages are not so tight.

EM fungus communities are impressively diverse, even for a plant genus such as *Alnus* that is associated with a species-poor group of fungi exhibiting narrow host specificity. Both of these studies report that while the depauperate EM fungal community associated with *Alnus* allowed better insight into the factors contributing to species distributions, the majority of community variation remained unexplained by the parameters investigated. Further, neither study exhausted the species-effort curve and we do not know which MOTUs may have been at a site but not sampled. We therefore suggest that inferences about the effects of host, edaphic and climatic factors on EM fungal community diversity should be made cautiously. Still, several key lessons emerge from these studies. Both showed (1) a variety of factors correlated with fungal diversity at different spatial scales; (2) fungal species vary in their response to these factors; (3) the fungi associated with *Alnus* range from those that associate freely with any available *Alnus* species to those that are specific at the subgenus level; and (4) co-migration has created strong linkages between plant histories and fungal diversity.

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References

- Anderson MD, Taylor DL, Ruess RW. 2013. Phylogeny and assemblage composition of *Frankia* in *Alnus tenuifolia* nodules across a primary successional sere in Interior Alaska. *Molecular Ecology*, in press.
- Bascompte J, Jordano P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics* 38: 567–593.
- Bruns TD. 1995. Thoughts of the processes that maintain local species diversity of ectomycorrhizal fungi. *Plant and Soil* 170: 63–73.
- Hoeksema JD. 1999. Investigating the disparity in host specificity between AM and EM fungi: lessons from theory and better-studied systems. *Oikos* 84: 327–332.
- Martos F, Munoz F, Pailler T, Kottke I, Gonneau C, Selosse M-A. 2012. The role of epiphytism in architecture and evolutionary constraint within mycorrhizal networks of tropical orchids. *Molecular Ecology* 21: 5098–5109.
- Molina R, Massicotte H, Trappe JM. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen MF, ed. *Mycorrhizal functioning an integrative plant–fungal process*. New York, NY, USA: Chapman and Hall, 357–423.
- Pölme S, Bahram M, Yamanaka T, Nara K, Dai YC, Grebenc T, Kraigher H, Toivonen M, Wang P-H, Matsuda Y, Naadel T, Kennedy PG, Köljal U, Tedersoo L. 2013. Biogeography of ectomycorrhizal fungi associated with alders (*Alnus* spp.) in relation to biotic and abiotic variables at the global scale. *New Phytologist* 198: 1239–1249.
- Roy M, Rochet J, Manzi S, Jargeat P, Gryta H, Moreau P-A, Gardes M. 2013. What determines *Alnus*-associated ectomycorrhizal community diversity and specificity? A comparison of host and habitat effects at a regional scale. *New Phytologist* 198: 1228–1238.
- Thompson JN. 1994. *The coevolutionary process*. Chicago, IL, USA: University of Chicago Press.
- Trappe JM. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. *Annual Review of Phytopathology* 15: 203–222.
- Vanderplank JE. 1978. *Genetic and molecular basis of plant pathogenesis*. New York, NY, USA: Springer-Verlag.
- Vincenot L, Nara K, Stultz C, Labbe' J, Dubois M-P, Tedersoo L, Martin F, Selosse M-A. 2012. Extensive gene flow over Europe and possible speciation over Eurasia in the ectomycorrhizal basidiomycete *Laccaria amethystina* complex. *Molecular Ecology* 21: 281–299.

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