

Meetings

Individuals, populations, communities and function: the growing field of ectomycorrhizal ecology

21st New Phytologist Symposium: The ecology of ectomycorrhizal fungi, Montpellier, France, December 2008.

The 21st New Phytologist symposium entitled 'The ecology of ectomycorrhizal fungi' attracted over 100 participants to Montpellier, France, for a two-day meeting in early December. Marc-André Selosse (Université Montpellier, France) and Ian Alexander (University of Aberdeen, UK) organized the talks around the classic ecological hierarchy of individuals, populations and communities. The meeting also struck a balance between trying to apply broad ecological theory to ectomycorrhizal fungi and investigating the unique aspects of the organisms and the interactions involved.

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Mark Fricker's (Oxford University, UK) innovative work on fungal networks provided an excellent example of the type of organism-specific research that is crucial to the field. His time-lapsed, false-color videos of the movement of radioactively labeled carbon-containing and nitrogen-containing compounds captivated the audience. The finding of oscillatory pulses in fungal transport and their synchrony when networks fuse was particularly striking and required the development of sophisticated image analyses to be demonstrated (Fricker *et al.*, 2007). All of his work has thus far been conducted using

saprobic fungi, but it is likely to be highly applicable to ectomycorrhizal systems.

Population ecology

In the symposium's introduction, Ian Alexander (University of Aberdeen, UK) noted that population ecology has not been well represented in the field of ectomycorrhizal ecology but the organizers arranged for three talks to review recently published work. Andre Rubini's (Plant Genetics Institute, Perugia, Italy) presentation on the economically important truffles, *Tuber magnatum* and *Tuber melanospora*, provided an excellent example of how population genetics can lead to autecological knowledge. Early studies on *T. magnatum* had suggested that the species was characterized by selfing because single sporocarps always appeared to be homozygous for polymorphic markers (Bertault *et al.*, 2001). However, Rubini showed that this result was an artifact of the DNA-extraction method that preferentially extracted the haploid parental tissue and failed to extract the recombinant thick-walled ascospores. After adapting more vigorous extractions methods, it was found that that populations were outcrossing, diverse and geographically structured (Paolocci *et al.*, 2006, Riccioni *et al.*, 2008). Similarly, Annette Kretzer (SUNY-ESF, NY, USA) used microsatellite markers to explore the autecology of two false-truffles in the genus *Rhizopogon* and showed that they differed from each other in the size of their vegetative individuals (i.e. genets). This result was extended in a poster by Beiler *et al.* (University of British Columbia, Canada) who simultaneously genotyped roots of individual trees and showed that individuals of both *Rhizopogon* species associated with multiple trees. Kretzer also applied refined analytical methods to try to discern parent/offspring relationships among the *Rhizopogon* genets, but had limited success as a result of the resolution provided by the markers available (Kretzer *et al.*, 2005). However, the posters by Labbé *et al.* (INRA/Nancy Université, France) and Vincenot *et al.* (Université Montpellier, France) on *Laccaria* species showed that as the genomic era unfolds, the days of limited resolution may be over. Making use of the entire genome of *Laccaria bicolor*, they developed a large number of simple sequence repeat markers in both *L. bicolor* and *Laccaria amethystina* and applied these to Eurasian collections of *L. amethystina*.

It became clear from discussions that few generalizations could be made about fungal populations. Some fungi, such as *Tuber* and *Rhizopogon*, show geographic structure on a fairly fine scale, and others, such as *Laccaria*, have large well-mixed

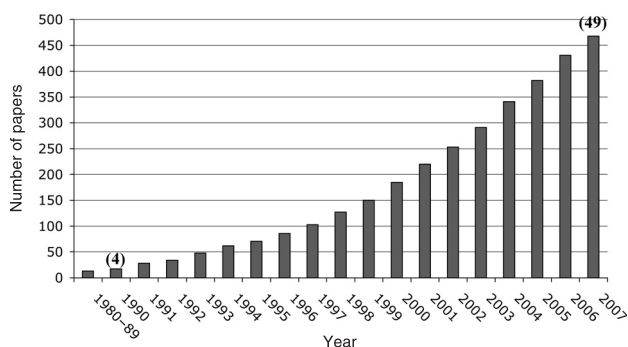


Fig. 1 Accumulation of publications on ectomycorrhizal community ecology. The results are from a Biosis search for Ectomycorr* and Commun* and Ecol*. Almost 500 papers have now been published on the subject. Forty-nine of these were in the last completed year (2007), compared with four in 1990.

populations across Europe. Is this caused by differences in the mode of spore dispersal (i.e. animals vs wind)? Or will this pattern break down as more species are sampled? However, the presence of cryptic species (i.e. species that look nearly identical but are genetically isolated) appears to be widespread in fungi. Kretzer's two *Rhizopogon* species were an example of this, as they were originally thought to be a single species. Many additional examples were provided in Greg Douhan's (University of California, Riverside, USA) and Andy Taylor's (Macaulay Institute and University of Aberdeen, UK) presentations. Taylor's talk was especially interesting because he showed many examples of cryptic species in the genus *Xerocomus*. As if to underline how poorly known these common fungi are, one of his undescribed species was found right in Silwood Park (Taylor *et al.*, 2007), but more interestingly, most of these species had distinct geographic distributions and host preferences. Using molecular clock estimates, Taylor postulated that these geographic distributions fit with distinct geological events, such as the final split up of Laurasia (60 million years ago) or the more recent Beringia land bridge (14 000 years ago), and he thus tied their autecology back to more general biogeographic patterns.

Community ecology

Ectomycorrhizal community ecology has received more attention than any other subdiscipline within the field. Publications on the topic have exhibited a 12-fold increase over the last 20 yr (Fig. 1). Progress in this area is largely a result of the increased ability to identify and quantify ectomycorrhizal fungi below ground using molecular methods (Horton & Bruns, 2001). While the patterning of ectomycorrhizal communities has been documented in increasing detail, this subdiscipline has been lacking a global perspective (Dickie & Moyersoen, 2008) and a mechanistic or theoretic understanding of what drives community assembly and structure.

Host-plant richness has long been thought to influence ectomycorrhizal community structure and diversity significantly, and a meta-analysis by Dickie (2007), supported this idea by identifying a strong, positive correlation between the richness of host plants and ectomycorrhizal fungi. However, few studies explicitly examined if the phylogenetic diversity of host plants correlates with ectomycorrhizal community structure and diversity. Kazuhide Nara (University of Tokyo, Japan) presented recent work showing that ectomycorrhizal communities on phylogenetically similar hosts were significantly more similar to each other than those on less closely related hosts (Ishida *et al.*, 2007), and found that this correlation was caused mostly by host preference rather than absolute specificity. To determine if similar richness relationships were present in tropical forests, Dr Nara examined the ectomycorrhizal community structure and diversity in an Indonesian dipterocarp-dominated forest with high host-plant diversity. He found that ectomycorrhizal diversity was much lower than predicted from temperate studies and that his results were similar to those of the handful of other studies carried out on tropical ectomycorrhizal communities (Tedersoo *et al.*, 2007). If this pattern holds, it has major implications for the larger field of ecology because it would indicate that ectomycorrhizal fungi represent a rare exception to the negative correlation between diversity and latitude. Confirming this result and understanding why ectomycorrhizal diversity patterns may differ from other organisms are clearly ripe areas for future research.

Community ecology is certainly a well-developed field in other systems, and dispersal, environmental conditions and biotic interactions have all been shown to play important roles in the assembly and dynamics of plant and animal communities. Peter Kennedy (Lewis and Clark College, USA) examined the roles of these factors in ectomycorrhizal communities and suggested that their relative importance in community assembly is both spatially and temporally scale-dependent. He also presented work showing that the assembly of ectomycorrhizal communities can be strongly influenced by the order and spatial patterning of species arrival. Another example of the growing confluence between ectomycorrhizal and general community ecology was demonstrated by Sara Branco (University of Chicago, USA), whose poster won top prize at the symposium. Ms Branco used an ecophylogenetic approach (Webb, 2000) to examine the community dynamics of ectomycorrhizal fungi present in serpentine soils. She found strong phylogenetic clustering in comparisons between serpentine and nonserpentine communities, but strikingly different patterns of clustering at the species and genus levels. From this part of the symposium, it was clear that the widespread adoption of molecular techniques has allowed ectomycorrhizal ecologists to describe many aspects of communities, but a combination of greater experimentation (particularly in the field) and theory-based research questions are now needed to move the subdiscipline towards greater synthesis and predictive ability.

Given the high diversity found in most ectomycorrhizal fungal communities, examining functional differences among species is important to integrate the parts of the aforementioned ecological hierarchy (Koide *et al.*, 2007). Jean Garbaye (INRA, Nancy, France) presented recent work linking taxonomic diversity with the diversity of enzymatic activity associated with individual ectomycorrhizal root tips. The method assays individual excised root tips for multiple enzymatic activities with a microtiter dish format (Courty *et al.*, 2005). At the community level, Garbaye demonstrated that rare ectomycorrhizal species often contributed disproportionately to total enzymatic activity, indicating their potential importance for ecosystem functioning. He also showed that enzyme activity varied considerably within species depending on environmental conditions, soil depth and time of year. A major attraction of this assay is that it has a very high throughput; however, the removal of extraradical hyphae during tip preparation creates an artifact that complicates comparisons among species. An alternative way to assay enzymatic activity under field conditions was presented by Brooks *et al.* (University of British Columbia, Canada) in a poster. This technique involved taking an imprint of the enzymes from a soil profile onto a membrane, assaying the activity of selected enzymes (in this case phosphatase) and correlating it with the ectomycorrhizal fungi or other organisms present at that particular point in the soil. While this method allows one to assay the contributions of extramatrical hyphae along with other soil organisms, it is not well suited to the same high-throughput analyses that the excised tip method offers. Thus, like other methods in this field, these approaches provide useful, but limited, views into this complex symbiosis.

The small meeting format and the limited number of talks provided many opportunities for lively discussions. These were enhanced by the frequent comments from Sir David Read (University of Sheffield, UK), whose voluminous work on mycorrhiza laid the foundation for much of the current research (Alexander, 2007). Overall, the continuity between past and present, methods and theory, and opinions and data made this meeting a productive step towards the future in this vibrant field. The program and the abstracts are available on the web for those who were unable to attend (<http://www.newphytologist.org/mycorrhizal/default.htm>).

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References

- Alexander I. 2007. A Knight of symbiosis. *New Phytologist* 176: 499–510.
- Bertault G, Roussett F, Fernandez D, Berthomieu A, Hochberg ME, Callot G, Raymond M. 2001. Population genetics and dynamics of the black truffle in a man-made truffle field. *Heredity* 86: 451–458.
- Courty PE, Pritsch K, Schloter M, Hartmann A, Garbaye J. 2005. Activity profiling of ectomycorrhiza communities in two forest soils using multiple enzymatic tests. *New Phytologist* 167: 309–319.
- Dickie IA. 2007. Host preference, niches and fungal diversity. *New Phytologist* 174: 230–233.
- Dickie IA, Moyersoen B. 2008. Towards a global view of ectomycorrhizal ecology. *New Phytologist* 180: 263–265.
- Fricker MD, Tlalka M, Bebbler D, Tagaki S, Watkinson SC, Darrah PR. 2007. Fourier-based spatial mapping of oscillatory phenomena in fungi. *Fungal Genetics and Biology* 44: 1077–1084.
- Horton TR, Bruns TD. 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. *Molecular Ecology* 10: 1855–1871.
- Ishida TA, Nara K, Hogetsu T. 2007. Host effects on ectomycorrhizal fungal communities: insight from eight host species in mixed conifer-broadleaf forests. *New Phytologist* 174: 430–440.
- Koide RT, Courty PE, Garbaye J. 2007. Research perspectives on functional diversity in ectomycorrhizal fungi. *New Phytologist* 174: 240–243.
- Kretzer AM, Dunham S, Molina R, Spatafora JW. 2005. Patterns of vegetative growth and gene flow in *Rhizopogon vinicolor* and *R-vesiculosus* (Boletales, Basidiomycota). *Molecular Ecology* 14: 2259–2268.
- Paolocci F, Rubini A, Riccioni C, Arcioni S. 2006. Reevaluation of the life cycle of *Tuber magnatum*. *Applied and Environmental Microbiology* 72: 2390–2393.
- Riccioni C, Belfiori B, Rubini A, Passeri V, Arcioni S, Paolocci F. 2008. *Tuber melanosporum* outcrosses: analysis of the genetic diversity within and among its natural populations under this new scenario. *New Phytologist* 180: 466–478.
- Taylor AFS, Hills AE, Simonini G, Munoz JA, Eberhardt U. 2007. *Xerocomus silwoodensis* sp. nov., a new species within the European *X. submentosus* complex. *Mycological Research* 111: 403–408.
- Tedersoo L, Suvi T, Beaver K, Koljalg U. 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpinaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). *New Phytologist* 175: 321–333.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* 156: 145–155.

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Mycorrhizas in tropical forests: a neglected research imperative

Mycorrhizas in Tropical Forests, a workshop held at Universidad Técnica Particular de Loja (UTPL), Loja, Ecuador September, 2008

Mycorrhizal research in tropical forest has a long history. Janse's (1896) paper of 'Les endophytes radicaux de quelques