

Meetings

Sharing resources for mutual benefit: crosstalk between disciplines deepens the understanding of mycorrhizal symbioses across scales

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Mycorrhizal scientists from 53 countries gathered in the city of Prague from 30 July until 4 August 2017 for the 9th International Conference on Mycorrhiza (ICOM9). They came to discuss an ancient symbiosis based on the exchange of resources between plant and fungal partners, with many impacts on plant health (van der Heijden *et al.*, 2015). Much like this mutualistic interaction, delegates from disparate disciplines united with a strong focus on integration and sharing of resources for mutual benefit. By exchanging knowledge among researchers from the fields of molecular biology, physiology and ecology, the participants of ICOM9 made a leap forward in our understanding of symbiotic structure and function at multiple scales (Fig. 1).

Evolution of the symbiosis and flexibility in lifestyles

Mycorrhizal fungi are an evolutionary success story, forming symbioses with the majority of terrestrial flora. Arbuscular mycorrhizal (AM) fungi first colonized the primitive rooting structures of plants, such as liverworts, *c.* 400 million years ago, facilitating plant emergence onto land (reviewed in Martin *et al.*, 2017). It is generally accepted that these early fungi were from the clade Glomeromycotina, but Katie Field (Leeds University, UK) challenged this hypothesis. She presented evidence that arbuscule-forming Mucoromycotina, a sister group of Glomeromycotina, have a much greater phosphorus (P)-for-carbon (C) exchange efficiency across a wide range of CO₂ levels. This would have made them better partners than the Glomeromycotinans in the comparatively higher CO₂ levels during the Palaeozoic Era (Field *et al.*, 2016). In line with this, new research by Suzanne Orchard (University of Western Australia, Australia) suggests that Mucoromycotina also may form arbuscules in roots of higher plants (Orchard *et al.*, 2017).

The ectomycorrhizal (EcM) symbiosis evolved later, *c.* 175–200 million years ago. EcM were first found in Pinaceae, and are today found in at least 30 independent plant lineages world-wide, as presented by Leho Tedersoo (University of Tartu, Estonia; Tedersoo & Brundrett, 2017). This evolution was likely driven by both plants and fungi: plants needed new strategies for nitrogen

acquisition as they developed more complex life forms, ecologies and functions in a changing landscape (Brundrett, 2017). From the fungal perspective, EcM potentially evolved in a lignin-rich environment, where the energy return of decomposition was low and symbiotic lifestyles were therefore advantageous over saprotrophy.

Losses of the mycorrhizal lifestyle took place in some plant lineages more recently, *c.* 70 million years ago, when plants evolved more complex root traits, such as cluster roots, allowing them greater ability to acquire soil nutrients autonomously in specific, extreme conditions (Lambers & Teste, 2013). Gijsbert Werner (University of Oxford, UK), who performed ancestral state reconstruction analyses with > 4000 plant species, suggested that increasing soil nutrient levels and decreasing temperatures drove the loss of AM status.

Comparative genomics has shed light on the evolution of mycorrhizal fungal groups with diverse and sometimes flexible lifestyles. For example, Francis Martin (INRA, Nancy, France) and Lazslo Nagy (Biological Research Centre Szeged, Hungary) presented genomic analyses of a large variety of fungal taxa, illustrating the loss of genes encoding plant cell wall degrading enzymes (lignocellulolytic enzymes) and the recruitment of genes involved in mycorrhiza formation in most EcM fungal genomes (Kohler *et al.*, 2015). Elena Martino (University of Turin, Italy/INRA Nancy, France) showed that ericoid mycorrhizal fungi possess the genetic potential to degrade complex substrates, suggesting that they can live as saprotrophs as well as plant endosymbionts. These genes are not found in Glomeromycotina, which for long have been understood to acquire all of their C from plant-derived carbohydrates. However, Maria Harrison (Boyce Thomson Institute, USA) and Caroline Gutjahr (Ludwig-Maximilians Universität München, Germany) convincingly showed that AM fungi are able to utilize C forms other than carbohydrates, and are actually fatty acid auxotrophs, receiving lipids from their host plants in order to synthesize fatty acids (Bravo *et al.*, 2017; Keymer *et al.*, 2017).

Despite their different evolutionary histories and C acquisition strategies, AM and EcM symbioses share more similarities in their signaling pathways than expected. Jean-Michel Ané (University of Wisconsin-Madison, USA) reported that basic signaling pathways, well known from the AM symbiosis, involving lipo-chito-oligosaccharide (LCO) production by fungi and calcium-spiking response in roots, is present, active and even required for EcM formation. The evolutionary connection between these pathways in AM and EcM symbioses remains to be shown, and one may keep an eye on idiosyncrasies of the ECM symbiosis.

Scaling up from pairwise interactions to higher levels of complexity

Although our understanding of molecular mechanisms and physiological processes underlying the mycorrhizal association has increased substantially, much of our knowledge is based on

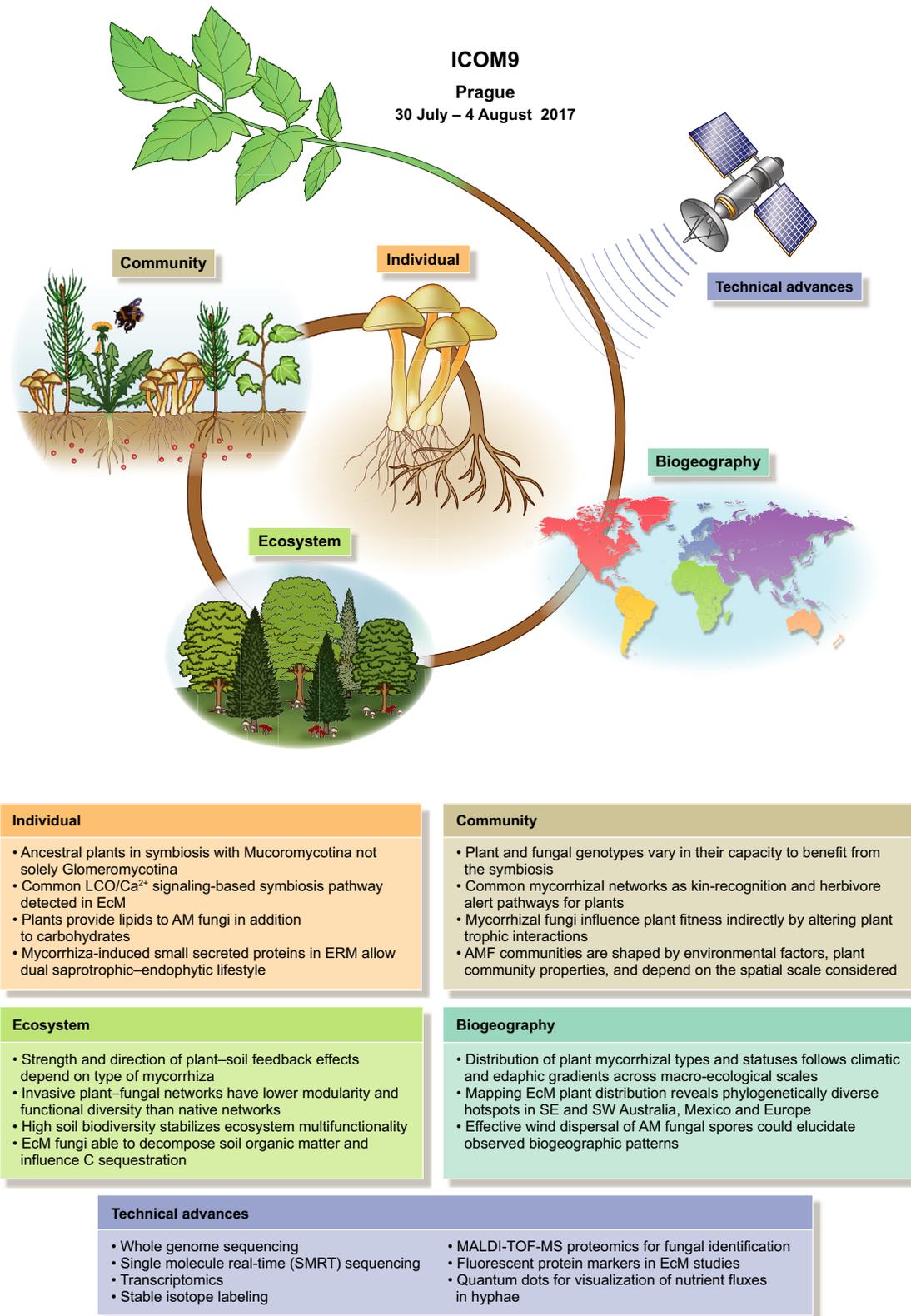


Fig. 1 ICOM9 advanced our understanding of symbiotic structure and function at multiple scales. AMF, arbuscular mycorrhizal fungi; EcM, ectomycorrhiza; ERM, ericoid mycorrhiza.

single plant–single fungus systems. It is a great challenge to scale up from these simple interactions to community or ecosystem levels, where multiple individuals of multiple species are interconnected and plant–fungal networks are the rule (Selosse *et al.*, 2006). Many

presenters at ICOM9 illustrated how these complex interactions can influence this symbiosis.

Interactions with bacteria in the mycorrhizal microbiome can affect the nutrient uptake ability of the fungi. Some current research

indicates that rhizospheric bacteria can transform organic C in the soil into less complex forms that can be used by the fungi, thus improving mycorrhizal resource acquisition (Jansa *et al.*, 2013). By contrast, Carla Cruz-Paredes (University of Copenhagen, Denmark) showed that some bacteria that are present in acidic soils can have a negative impact on AM fungi, reducing their phosphate uptake activity.

Mycorrhizal fungi can also mediate the interactions between plants and their antagonists in ways that affect plant distribution and performance. For example, Andrea Polle and her colleagues (Georg-August-Universität, Göttingen, Germany) found that the EcM fungus *Laccaria bicolor* induced metabolic changes in poplar (*Populus × canescens*) plants that resulted in reduced feeding damage and oviposition by the specialist herbivorous insect *Chrysomela populi* (Müller *et al.*, 2015). Jonathan Bennett (University of British Columbia, Canada) reported that AM and EcM fungi moderate plant–soil feedbacks differently and linked this with population dynamics in temperate forests. Plant–soil feedback refers to the impact of plants on the composition of the soil community, that in turn influences the growth of conspecific plants (Bever *et al.*, 1997). Using 55 different tree species and 550 populations, he showed that trees in EcM-dominated systems are more likely to benefit from positive soil feedbacks, presumably due to nutritional benefits from specific fungal associations, whereas hosts in AM-dominated systems are more likely to suffer from negative soil feedback, due to pathogen accumulation (Bennett *et al.*, 2017). These findings suggest that differences in the way distinct types of mycorrhizal associations mediate protection from pathogens and potentially other antagonists can drive plant diversity in temperate forests.

It is clear that plants and their mycorrhizal fungal partners interact in a complex network with multiple other species, which can influence many community and ecosystem attributes. However, understanding how complex interaction networks actually influence these processes (and vice versa) can be a challenge. Marcel van der Heijden (Agroscope and University of Zurich, Switzerland) used network imagery to show how different farming systems (organic vs conventional) shift microbial co-occurrence networks in ways that affect their function. Ian Dickie (University of Canterbury, New Zealand) used a network approach to show that many exotic tree species in New Zealand tend to interact with a distinct set of fungi compared with native tree species (Dickie *et al.*, 2017a,b).

A functional perspective on the distribution of plants and fungi across multiple scales

Advances in molecular methods have enabled us to detect and map mycorrhizal fungi and plants across continents and biomes in an unprecedented manner (e.g. Jacquemyn *et al.*, 2017; Tedersoo & Brundrett, 2017), but the driving forces behind these distribution patterns are still unclear. Incorporating the functional traits of mycorrhizal fungi and their hosts is a promising approach for tackling the challenge of understanding what drives the observed multi-scale distributional patterns.

Plant mycorrhizal trait data, such as the mycorrhizal type, degree of dependency and flexibility of the relationship can be used to understand the distributional patterns of plants and fungi across multiple spatial scales. Mari Moora (University of Tartu, Estonia) correlated these traits with data on the large-scale distribution of the mycorrhizal symbioses and showed that obligate mycorrhizal plants prevail in southern latitudes while facultative and nonmycorrhizal plants are more likely to occur in northern latitudes of Europe (Bueno *et al.*, 2017). Dependency and specificity in associations between partners can also influence the local distributions of plants. This is particularly the case for plants such as orchids, which are dependent on mycorrhizal symbionts for germination or establishment. Melissa K. McCormick (Smithsonian Environmental Research Center, USA) showed that the local distribution patterns of orchid populations were strongly linked to the distribution and abundance of their associated mycorrhizal fungi in soil (McCormick *et al.*, 2016). When focusing on six both rare and common orchid species, Tamara Těšitelová and colleagues (University of South Bohemia, Czech Republic) found that only two common orchid species with low fungal specificity germinated in restored meadows, while the others germinated only in undisturbed natural grasslands with established orchid populations. Taken together, these results suggest that the abundance and diversity of mycorrhizal fungi in soil may be one of the factors limiting the establishment of some orchid species.

Trait data can also be used to understand how the environment shapes plant and fungal distribution. Jeff Powell (West Sydney University, Australia) correlated plant and fungal (i.e. spore) traits with abiotic variables, to understand how environmental filtering shapes AM fungal distribution. Synnøve Botnen (University of Oslo, Norway) used a similar approach and showed that EcM fungal spore shape and mycelial exploration types correlated with climatic variables. Bala Chaudhary (DePaul University, USA) used a novel technique to explore how wind disperses AM fungal spores over long distances and linked this with specific spore traits. These findings could explain the low level of endemism found in recent work on global patterns of AM fungi (Davison *et al.*, 2015).

Exciting advances have been made in modeling studies which predict how distributions of plants and mycorrhizal fungi may change over time. Colin Averill (Boston University, USA) collected mycorrhizal trait data from 3000 US forest inventory plots to model how forest plant communities associated with particular mycorrhizal types are shifting alongside anthropogenic global changes. His models predict a decreasing abundance of EcM compared to AM hosts, as N-deposition increases over large spatial scales. Given the differences in the way the different mycorrhizal types influence soil C stabilization, these shifts could impact global C cycling. Gaby Deckmyn (University of Antwerp, Belgium) presented a model predicting thresholds in the P-limitation of forests while incorporating interactions with EcM fungi. These studies reveal the importance of compiling information on both plant and fungal distribution and traits, to better understand how abiotic and biotic factors drive the distribution of species. These studies can help us to predict how the symbiosis will respond to a changing environment.

Conclusions

ICOM9 brought together many perspectives and fresh ideas from a broad range of spatial and organizational scales (Fig. 1). Catherine Gehring (Northern Arizona University, USA) reviewed the advances made in every scale of the organization of mycorrhizal science, and found that over 1700 papers on mycorrhizas have been published over the 2 years since the last ICOM. However, at a time of rapidly developing technologies, Thorunn Helgason (University of York, UK) cautioned us to question: 'What data do we actually need?' instead of 'What data can we get?'. Roger Koide (Brigham Young University, USA) reminded us of the perspectives of John Laker Harley, a pioneer in the field, who understood the importance of sharing ideas, reviewing our own work more critically, and of bringing together seemingly disparate concepts to form a synthesis. Ian Sanders (University of Lausanne, Switzerland) echoed this sentiment, advocating that we, as the scientific community, should continue to talk to each other but need to learn to speak the same language. Roger Koide used the metaphor of streams coming together to form a larger river, to illustrate an integrated approach to mycorrhizal research going forward: reciprocal trade of resources that are limiting to one partner but not the other will make the stream grow larger.

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