Editorial

Evolving insights to understanding mycorrhizas

Almost all land plant species form a symbiosis with mycorrhizal fungi. These soil fungi provide nutrients and other services to plants in return for plant carbohydrates. The recent application of microbial metagenomics, metatranscriptomics, and metabolomics to plants and their immediate surroundings confirms the key role of mycorrhizal fungi, rhizosphere bacteria and fungi, and suggests a world of hitherto undiscovered interactions (van der Heijden *et al.,* this issue, pp. 1406–1423). This novel knowledge is leading to a paradigm-shifting view: plants cannot be considered as isolated individuals any more, but as metaorganisms, or holobionts (Hacquard & Schadt, this issue, pp. 1424–1430) encompassing an active microbial community re-programming host physiology (see Pozo *et al.,* this issue, pp. 1431–1436). This bears tremendous implications for plant ecophysiology and evolution, plant breeding, crop management and sustainable ecosystem management.

Mycorrhizal associations are centerpieces in this wide cortege of plant-associated soil biota. To exploit these evolving insights, critical gaps need to be filled in our current understanding of mycorrhizal interactions. This special issue of *New Phytologist* addresses fundamental gaps and contains 30 new contributions on mycorrhizal science, covering topics from genomes to ecosystems. These contributions result from the 33rd New Phytologist Symposium *Networks of power and influence: ecology and evolution of symbioses between plants and mycorrhizal fungi* (Zürich, 14–16 May 2014, http://www.newphytologist.org/symposiums/view/4; see also Bender *et al.*, 2014).

A series of key questions addressed in this issue explore some of the most cutting-edge approaches, and include: (1) How is the balance of mutualism maintained between plants and fungi? (2) What is the role of mycorrhizal fungi in the soil ecosystem? (3) What controls fungal community composition, and how is diversity maintained? While many of these questions originated in the earliest days of mycorrhizal science (Koide & Mosse, 2004), the development of new tools and approaches, from genomics to mathematical models to isotopes, is allowing them to be addressed in greater detail, clarity and depth than ever before.

The balance of mutualism and partner selection

From the earliest days of mycorrhizal science, a perennial question has been the balance of mutualism and parasitism (Bronstein *et al.*, 2014), particularly in arbuscular mycorrhizas (AMs)

(Koide & Mosse, 2004). As obligate symbionts, the fungal partners in AM always benefit (Smith & Smith, this issue, pp. 1381–1384), but benefits for the plant partner can vary substantially with environmental conditions (Johnson *et al.*, this issue, pp. 1473–1484), and depending on host–plant identity and development. Maintaining symbiosis in the face of the variable benefits received, depends on the ability of plant and fungal partners to select for or against one another (Werner & Kiers (2015a), this issue, pp. 1437–1442), and to avoid interaction with 'cheaters', fungi or plants that acquire resources from the mutualism without providing reciprocal rewards. The best approaches to understanding these interactions and explaining plant–fungal coexistence remain unclear. Werner & Kiers (2015a) argue that these processes can be best understood by the biological market theory (Noe & Hammerstein, 1994), where each individual can change partner on the basis of benefits supplied by other partners, as in human market economy. While not explicitly using market theory, Engelmoer & Kiers (this issue, pp. 1485–1491) provide, using *in vitro* root cultures, an elegant example of how a market prediction, that is, that plants connected in a mycorrhizal network should reduce investment to avoid benefiting competing plants, can be directly tested. Despite being based on relatively simple market analogies, this provides a novel understanding of mycorrhizal hyphal networks from a fungal view. Further work should now test carbon allocation to mycorrhizal networks in plant–soil systems where plant carbohydrate availability differs from those in *in vitro* root cultures.

While the market analogy can clearly serve a purpose, Smith & Smith and van der Heijden *et al.* raise important cautions about extending the market analogy for mycorrhizal mutualisms beyond the discussion of general principles. There are a number of important aspects of the mutualism that the market analogy fails to capture. One, raised by Smith & Smith, is the issue of mycoheterotrophs (see Field *et al.*, this issue, pp. 1492–1502), and so-called 'cheaters'. Indeed, there is evidence for manipulations of host gene expression by colonizing fungal symbionts through effector proteins (Plett *et al.*, 2014), opening the way to manipulation of the market. Bever (this issue, pp. 1503–1514) shows how a mechanistic model helps to provide greater insight into these interactions. The simple assumption that plants must be first colonized by fungi before being able to assess their symbiotic efficiency, provides a mechanism whereby less efficient fungal symbionts can persist over a relatively wide range of environmental conditions. Field *et al.* further extend the importance of considering plant–fungal exchanges over the whole lifespan of the association, showing that the mycoheterotrophic fern *Ophioglossum vulgatum* has developed a 'take now, pay later' strategy, being entirely dependent on fungi for both nutrients and carbon as a gametophyte and young sporophyte, but potentially repaying this investment as mature sporophytes.

There are a number of additional concerns about the market analogy and the application of economic theory to symbioses. First, the application of market theory to mycorrhizal symbioses has frequently assumed a two-goods market, involving carbon and phosphorus. While some have argued that different types of resources (nitrogen, phosphorus, carbon) are analogous to multiple different currencies in markets (Bloom *et al.*, 1985), this analogy fails to recognize two aspects of plant physiology. First, mycorrhizal benefits are diverse for the plant (Selosse & Rousset, 2011), and plant protection by mycorrhizal fungi is also relevant (Newsham *et al.*, 1995): for example, in this issue, Pozo *et al.* examine the mechanisms by which mycorrhizas shape plant defense against pathogens and stress. Second, one essential nutrient simply cannot serve the same purpose or be exchanged for another: this fundamental principle underpins 'Liebig's law of the minimum' (Johnson, 2010), which has, despite some limitations, become one of the foundations of environmental stoichiometry. In this issue Johnson *et al.* integrate Liebig's law and stoichiometric theory with plant–fungal interactions in mycorrhizas, showing how the carbon: phosphorus exchange between plants and AM fungi breaks down when nitrogen is the main limiting nutrient.

Another major limitation of market theory is that the fungal community associating with a plant does not simply respond to plant resource allocation under market rules, but is also shaped by direct antagonistic competition among fungal species, as well as interactions with fungivores, pathogens of fungi, other soil biota and stochastic events. One example of this is the effect of assembly history, where the order of fungal species' arrival into an ecosystem determines community composition (Kennedy & Bruns, 2005; Dickie *et al.*, 2012; Peay *et al.*, 2012). This has also been shown for AM, where the fungal species that colonizes the root system first is able to effectively prevent or reduce colonization by later fungi (Abbott & Robson, 1984; Werner & Kiers (2015b), this issue, pp. 1515–1524). Werner & Kiers (2015b; see also Commentary by Johnson *et al.*, in this issue, pp. 1375–1377) discuss preferential allocation by hosts as potential mechanisms, but it is notable that other fungal systems also show priority effects in the absence of any host allocation (e.g. Dickie *et al.*, 2012; Peay *et al.*, 2012). This may imply that we should give more consideration to competition and direct fungal–fungal antagonism in mycorrhizal fungi; a mechanism that falls well outside traditional market theory or the mechanistic models of Bever. Finally, most current works use growth or nutrient flow as markers for the mutualism, but these are only proxies: in the future, a more evolutionary-relevant view of mutualism (or cheating) should ideally investigate the partners' fitness, that is, the ability to survive and reproduce.

Role in soil carbon

The carbon allocated by plants to mycorrhizas does not just support the fungus, but also has potentially profound effects on the soil ecosystem. Up to 50% of plant carbon is allocated to mycorrhizal fungi, pointing to the key role of mycorrhizal fungi in the carbon cycle (van der Heijden *et al.*). The recent finding that carbon sequestration in soil is related to mycorrhizal fungal community shifts during succession further points to the key role of mycorrhizal

fungi for the carbon cycle (Clemmensen *et al.*, this issue, pp. 1525–1536; see also the Commentary by Fernandez & Kennedy, this issue, pp. 1378–1380). A particularly vexing question in mycorrhizal ecology is the question of how carbon allocation to mycorrhizal fungi influences decomposition and the interaction of mycorrhizal fungi with free-living saprotrophs and litter decomposition. Using NanoSIMS imaging, Kaiser *et al.* (this issue, pp. 1537–1551) show the remarkably fast transfer of carbon from host plants to mycorrhizal hyphae, and out into the soil. The exudation of carbon by hyphae, rather than passive root exudation, may allow for much greater precision in using plant photosynthate to facilitate saprotrophic release of organic matter (the so-called priming effect).

Carbon exudation is not the only major pathway of mycorrhizal influence on soil carbon, as mycorrhizal fungi can both participate directly in decomposition (Lindahl & Tunlid, this issue, pp. 1443–1447), and form a substantial carbon pool in their own necromass (Clemmensen *et al.*; Fernandez & Kennedy). These effects are context dependent. In young, relatively nutrient-rich soils the net effect of mycorrhizal fungi on decomposition may be positive through priming and provision of an easily decomposable biomass. In older soils, on the contrary, the net effect of mycorrhizas may be to slow decomposition through the removal of nutrients, which become limiting for other microbes, and more decay-resistant hyphae (Orwin *et al.* 2011; Clemmensen *et al.*). Indeed, an important emerging theme in mycorrhizal research is the importance of fungal traits in predicting effects on ecosystem function (Clemmensen *et al.*; Rillig *et al.*, this issue, pp. 1385–1388).

While significant amounts of carbon pass through mycorrhizal networks, the direct contribution of mycorrhizas to decomposition and the breakdown of organic matter is still poorly documented. The repeated, independent evolutions to the mycorrhizal lifestyle in all fungal lineages are associated with a massive loss of lignocellulose-degrading genes compared to saprotrophic ancestors (Plett & Martin, 2011; van der Heijden *et al.*), suggesting a limiting role for decomposition. However, it appears that several ecto-mycorrhizal fungi potentially decompose organic matter through the oxidative cleavage of glycosidic bonds in cellulose and hemicellulose, and the oxidative modification and arrangement of lignin upon attack by highly destructive oxygen reactive species (Rineau *et al.*, 2013). They do not acquire carbon from this decomposing activity but mobilize nitrogen compounds embedded in organic matter thanks to a constant host carbohydrate supply (Lindahl & Tunlid). Acquisition of bacterial genes coding for decomposing enzymes through horizontal gene transfer can complement the enzyme arsenal of symbionts, and likely played a role in the evolution of mycorrhizal symbioses (Chaib De Mares *et al.*, this issue, pp. 1552–1564).

Communities and ecosystems

Another long-standing question in mycorrhizal science has been what determines the diversity, structure and composition of fungal communities. Molecular methods, allowing easier and faster detection and identification of fungi, are now driving a revolution in our understanding of fungal communities. Lindahl *et al.* (2013) compiled a user's guide for fungal community ecologists who use

amplicon-based next-generation sequencing (NGS), outlining many of the aspects of NGS technologies that need to be addressed to prevent making biased conclusions. In this issue, Nguyen *et al.* (pp. 1389–1393), follow on the theme, targeting the various aspects of contamination and need for controls in sample handling and NGS data production practices. The awareness of the problems outlined by them, with solutions offered, are of increasing importance as the data volume increases in line with the evolving NGS platforms.

The drivers of community dynamics of mycorrhizal fungi are only partly understood. Mycorrhizal fungal species distribution is influenced by external abiotic and biotic forces, and intrinsic fungal properties (Chaudhary *et al.*, 2008), but the role of biotic interactions (with host, other fungi and any other organisms) in shaping mycorrhizal fungal communities remains poorly investigated, and particularly little is known about co-variation of host and mycorrhizal fungal communities. Zobel & Öpik (2014) have proposed that in primary succession plant communities drive AM fungal communities (Passenger hypothesis), and in secondary succession (including in response to land use) the AM fungal community drives the plant community (Driver hypothesis). In successionally stable ecosystems both AM fungal and plant communities co-respond to local environmental gradients (Habitat hypothesis), but for large scales the two communities may have independent dynamics (Independence hypothesis). Empirical evidence is surprisingly scarce on these scenarios. Martínez-García *et al.* (this issue, pp. 1565–1576) now provide evidence that AM fungal communities across long-term ecosystem age gradients, from succession to retrogression, are strongly determined by ecosystem age and structured by host identity, thus providing support to the Passenger and/or Driver hypotheses.

AM fungal community responses to different land uses have been a topic of considerable interest since the demonstration of a dramatic decrease in AM fungal diversity in intensively managed arable fields in comparison to surrounding native vegetation (Helgason *et al.*, 1998). Vályi *et al.* (this issue, pp. 1577–1586) demonstrate that both land use and host plant identity affect AM fungal richness and community composition in a grassland system. Interestingly, the communities in this study were somewhat more taxon rich under high land-use intensity, which is counterintuitive considering the expected negative effect of land use. In agreement with this result, other managed ecosystems have turned out to be not necessarily depauperate in fungal species, both at local (Hijri *et al.*, 2006; Moora *et al.*, 2014) and larger regional scales (Xiang *et al.*, 2014). These results suggest that the response of AM fungal communities to the nature and intensity of land use may vary in direction, possibly in a context-dependent manner. The information we have on AM fungal diversity–disturbance relationships may represent different portions of the land-use intensity gradient. It may turn out that moderate disturbance supports the highest community diversity of these fungi while extremely low and extremely high disturbance negatively affects diversity, as has been proposed for other organisms by the 'intermediate disturbance hypothesis' (Hughes *et al.*, 2007).

The influence of abiotic drivers of mycorrhizal fungal communities remains idiosyncratic across studies. Mundra *et al.* (this issue,

pp. 1587–1597) found that while vegetation was structured by abiotic environmental parameters, the fungal communities associated with *Bistorta vivipara* roots were not. Bahram *et al.* (this issue, pp. 1454–1463) present a meta-analysis of mycorrhizal fungal communities of different types across temporal and different spatial scales, including vertical scales of soil depth. Perhaps surprisingly, they could not reveal clear trends except between top- and deeper-soil horizons. This further illustrates our fragmentary knowledge of mycorrhizal fungal diversity patterns at large scales, and suggests context-dependent, rather than uniform processes. Our ability, in the future, to gain clear views of fungal functional traits (Rillig *et al.*) will help the investigation of the processes acting in the establishment of fungal communities.

There are also important temporal components to mycorrhizal fungal communities, as illustrated by Cotton *et al.*'s (this issue, pp. 1598–1607) report of large interannual shifts in AM fungal communities in a soybean cropping system, which contrasts with the more limited interannual turnover observed in less disturbed ecosystems (Bennett *et al.*, 2013). Smaller, seasonal, shifts in orchid mycorrhizal fungal communities are reported by Oja *et al.* (this issue, pp. 1608–1618), whereas habitat and host species were stronger drivers of diversity patterns of these fungi in Estonian meadow and forest ecosystems. This study elegantly complements other recent insights into orchid mycorrhizal fungal community dynamics revealing host-related, spatial and temporal diversity patterns (Jacquemyn *et al.*, 2014; Ercole *et al.*, 2015) which were published in this journal after the 31st New Phytologist Symposium *Orchid symbioses: models for evolutionary ecology* (14–16 May 2013; Selosse, 2014; Bronstein *et al.*, 2014; http://www.newphytologist.org/symposiums/view/3).

Among the intrinsic properties of fungi, dispersal properties are deservedly gaining increasing interest. Dispersal limitation – the fact that not all suitable habitats are colonized by a species – has received increasing attention (e.g. Peay & Bruns, 2014). Another aspect of propagule availability is the pool of locally available, but not currently active organisms. In analogy with the plant seed bank concept, fungal spore banks (or propagule banks) in soil represent fungi that are currently dormant, but have the potential to start growing when suitable conditions appear. In this issue, Glassman *et al.* (pp. 1619–1631), provide evidence that ecto-mycorrhizal fungal spore banks represent a small subset of the mature forest's fungal community and are location dependent.

Conclusion: enlarging the mycorrhizal symbiosis to new players

Mycorrhizal symbiosis turns out to be a more complex network of interaction than often considered because new players enter the field. Lekberg *et al.* (this issue, pp. 1399–1403) challenge the status of nonmycorrhizal plants, suggesting that they could be relevant for AM fungi that colonize them. On the fungal side a new taxon was recently discovered to potentially join the scene: members of the Mucoromycotina were found to form associations with basal nonvascular land plants such as liverworts (Field *et al.*), sometimes together with AM fungi. Rimington *et al.* (this issue, pp. 1394–1398) now provide evidence that a wide range of basal vascular land

plants (ferns and lycopods) also associate with both AM and Mucoromycotina fungi. This is congruent with the recently described dual association with AM and Mucoromycotina fungi in a Devonian fossil plant (Strullu-Derrien *et al.*, 2014) whose phylogenetic position falls between liverworts and vascular plants. The colonization of Mucoromycotina, although obviously biotrophic (symptomless), raises the question of the physiological outcome on the plant side: although beneficial effects of Mucoromycotina have recently been demonstrated for liverworts (Field *et al.*), it deserves studies on more plant models, especially to test whether simultaneous colonization by both groups of fungi provide additional benefits. Bacterial players also enter the scene here: *Endogone*, a Mucoromycotina fungus, contains endosymbiotic bacteria (Desirò *et al.*, this issue, pp. 1464–1472), exactly as found in AM fungi (Ghignone *et al.*, 2012)), pointing to further similarities between these two lineages. The role, if any, of these bacteria in mycorrhizas also deserves further study.

On the plant side, the mycorrhizal symbiosis is increasingly viewed as an ecological network, where shared fungal partners create a common mycorrhizal hyphal network (Bender *et al.*, 2014) making each plant an indirect partner of its neighbors. Nutrient transfers are well known, as well as the imbalanced contribution of plant partners to mycorrhizal networks as compared to the benefit they gain, although the determinism for such outcome remains unclear (Walder *et al.*, this issue, pp. 1632–1645). New functions are now discovered: plant defense signals can be transferred from one plant to another through mycorrhizal networks as conduits (Johnson & Gilbert, this issue, pp. 1488–1453). Plants connected to networks are subsequently better protected against insect herbivores and antagonistic herbivores. Although the mechanisms, and the evolutionary forces that shape such indirect collaborations remain unclear, it is now evident that the mycorrhizal fungal community blurs the limits of plant holobionts.

Taken as a whole, the articles in this special issue represent a remarkable suite of studies, all focused on mycorrhizal science but ranging in scale from the molecular to covering whole-ecosystems. While the questions they address have a long legacy, the application of novel techniques and ideas has allowed significant advances in the understanding of this complex symbiosis. Mycorrhizal science has, perhaps more than many other fields of research, remained an integrated field; pulling together approaches from systematics, molecular biology, soil science, and ecology. This represents a significant strength of the field, and one that *New Phytologist* as a nonprofit trust has striven to support for many decades, in the pages of the journal and through symposia and workshops, in a lasting and deep-rooted 'love affair' (Selosse & Martin, 2013). *New Phytologist* will attend the 8th International Conference of Mycorrhiza (ICOM8), 3–7 August 2015, Flagstaff, AZ, USA, which represents the next step in this long-standing association.

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