



Editorial

Mycorrhizal diversity: Diversity of host plants, symbiotic fungi and relationships



Mycorrhizal symbioses are one of the most ubiquitous inter-organism relationships on the Earth, and particularly so in the terrestrial environment (Smith and Read, 2008). These relationships have major roles in the functioning of ecosystems, and are of large importance for humans via biodiversity maintenance, contribution to biogeochemical cycles, food and timber production, and other benefits (Gianinazzi et al., 2010; van der Heijden et al., 2015; Bender et al., 2016). Thus, thorough understanding of the diversity of mycorrhizal interactions—diversity of interacting plants, fungi, and diversity of mycorrhizal types—and ultimately on mycorrhizal functioning is timely.

This Special Issue contains six papers that were presented as oral or poster presentations at the 8th International Conference on Mycorrhizas (ICOM8) in Flagstaff, Arizona, August 3–7th 2015 (Chagnon et al., 2016), including presentations at the opening symposium of the conference, “Diversity and biogeography of mycorrhizal fungi”. The papers span an array of topics on mycorrhizal diversity: mycorrhizal types from arbuscular mycorrhiza (Lekberg and Waller, 2016; Öpik and Davison, 2016) to ectomycorrhiza (Lamit et al., 2016) and ericoid mycorrhiza (Leopold, 2016), the distribution of mycorrhizal types across the USA (Swaty et al., 2016), the diversity of mycorrhizal partners (Lekberg and Waller, 2016; Öpik and Davison, 2016; Swaty et al., 2016), and both theoretical (Chagnon, 2016) and empirical (Lekberg and Waller, 2016) approaches to disentangling host-fungal relationships across a range of genetic scales (Lamit et al., 2016). This fine sample of research topics, results, ideas and overviews reflects the remarkable contributions of mycorrhizal researchers to a breadth of research areas: from taxonomy to genetics and physiology, spatial scales ranging from cells to ecosystems, from individuals (autecology) to geochemical cycles, and the development of methodological approaches and ecological theory (e.g., Bever et al., 2010; van der Heijden et al., 2015; Moeller and Neubert, 2016; Peay, 2016).

1. The plant and the fungus

Mycorrhizal symbioses are known to vary in their level of host specificity, but recent years have seen the field take an increasingly nuanced view of specificity based on the relative strength of interactions between the two partners. For example, AM fungi were first thought to be host generalists, then selective towards host species, whilst now a selectivity on the basis of the partners' functional groups has been proposed (Helgason and Fitter, 2009; Koorem et al., 2016). Ectomycorrhizal systems, on the other hand, were

thought to be more specific in nature, with examples of strict specificity, for example between pines and *Suillus*, alder and *Alnicola*, and many examples of strong host-fungus correspondence in natural systems (Ishida et al., 2007; Tedersoo et al., 2008; Toju et al., 2016). However, recent work suggests that much of what appear to be host preferences may be independent assortment based on either shared environmental preferences or niche construction by the host (Miyamoto et al., 2015; Peay et al., 2015; Erlandson et al., 2016).

Here, Lamit et al. (2016) move beyond the traditional focus on different host species and explore how host genotype affects root-associated EcM fungal communities in a common-garden experiment with 15-year-old *Populus angustifolia* (poplar). They report different EcM fungal community compositions depending on the host genotype, and provide some evidence in support of leaf litter chemistry (measured as senescent leaf chemical composition) playing a role in this relationship. Major fungal players in this system are ascomycete EcM fungi. Furthermore, poplar is a dual mycorrhizal host, and one issue the authors were unable to address is the role that AM fungi may have played in generating these patterns. However, Lekberg and Waller (2016) explore a complementary question about AM fungi at the host species level, aiming to disentangle the drivers of the observed variation in AM fungal communities among host plant species. Interestingly, they found that host plant species harbour different AM fungal communities at only 25% of surveyed locations. This context dependent host specificity may help explain the numerous contradicting reports that there is a host effect on AM fungal communities (e.g., Vandenkoornhuys et al., 2002), or that there is none (e.g., Saks et al., 2014). Lekberg and Waller (2016) also found that richness of AM fungi was more likely to differ among host plant species than community composition. They explain this result in terms of resource supply, which for AM fungi is plant photosynthate. Indeed, there is recent evidence that availability of plant photosynthates may drive AM fungal diversity patterns (Koorem et al., 2016).

It is also noteworthy that Lekberg and Waller (2016) do not generate new data to explore their research question, but utilise a dataset made fully available by its original authors (Davison et al., 2015), and already reanalysed from several additional angles to, for example, identify different assembly rules of AM fungi operating at different spatial scales (Davison et al., 2016) or to describe the high level of variation of AM fungal communities associating with a host plant species (Powell and Bennett, 2016). In short, providing access to full datasets (raw and semi-

raw data) is beneficial for the scientific community, as the generated data can be maximally exploited. This is an increasing and welcome trend.

2. Ericoid mycorrhizal fungi

Leopold (2016) provides an overview of the current understanding of ericoid mycorrhizal (ErM) fungal diversity. ErM is a type of mycorrhizal association that is widespread but found in a smaller land area than other mycorrhizal types (Swaty et al., 2016). It has been thought to be confined to a narrow set of plant hosts and fungal symbionts, but the range of fungi involved in ErM symbiosis has turned out to be considerably larger than initially known. Leopold (2016) reviews the current knowledge of biodiversity of ErM forming fungi, spanning clades in Ascomycota and Basidiomycota, highlights the gaps in their known distribution (Southern Hemisphere in particular!), and outlines future research potential on key ecological questions using ErM, in particular considering the ease of culturing of many ErM fungi. Recent reports on members of Sebaciales forming ErM (Vohnik et al., 2016; Weiss et al., 2016), to pick just one example, show that there is more news on diversity of ErM fungi!

3. Arbuscular mycorrhizal fungi

Plants' relationships with mycorrhizal fungi started with arbuscular mycorrhizas (AM) when the ancestors of terrestrial plants first established in the non-aquatic environment, being ready to form symbioses (Delaux et al., 2015) and hosting AM fungal-like organisms (Strullu-Derrien et al., 2014). AM fungal ecosystems continue to be very widespread (Swaty et al., 2016). However, as Öpik and Davison (2016) outline, much is still to be learned about this symbiosis, and about AM fungal diversity. Öpik and Davison (2016) argue for the benefits of increasing consolidation of species- and community-oriented approaches for studying AM fungi, by both descriptive and experimental research. They also provide the current species list of Glomeromycota, now counting 289 species, to help the research community find their way in the maze of new names. Further, they introduce the species pool concept (Zobel, 2016) as a useful framework for studying AM fungal diversity patterns (Pärtel et al., 2016). They are not alone in doing so: evidence for there being sets of AM fungal species adapted to specific conditions, such as habitats (=habitat specific species pools), has been recently reviewed (Valyi et al., 2016). In other words, despite the extremely large ranges of many AM fungi, there seem to be discreet regional or habitat specific species pools, in the sense of species pool concept, that can now be identified using computational tools (Lewis et al., 2016). Understanding the ecological and evolutionary factors that are behind these species pools appears to be a newly promising approach to a deeper understanding of the diversity patterns of this important group of fungi (Öpik and Davison, 2016; Pärtel et al., 2016).

4. Networks

Network analysis is an increasingly popular method of depicting plant-fungal interactions in complex communities. However, the extent to which these statistical tools accurately represent ecological interactions is sometimes unclear. Chagnon (2016) reviews the pros and cons of the application of network theory and analytical tools for the respective analyses, in the case of mycorrhizal plant and fungal interaction networks. Doing so, contributes to a growing line of discussion about appropriate ways to apply the network framework tools to gain further understanding of mycorrhizal interactions (Caruso et al., 2012; Öpik and Moora, 2012; Balint

et al., 2016). This addition is particularly timely because of the striking increase in publications using the network analysis approach (Fig. 1 in Chagnon, 2016), reflecting the increasing availability of suitable data and data analysis tools. However, attention needs to be drawn to the assumptions and applicability of the approach. As Chagnon concludes, application of the network theory tools to analyse mycorrhizal interactions allows answering fresh questions, but care should be taken not to extrapolate beyond the limits of the data.

5. Put them on the map!

Swaty et al. (2016) tackle the near-continental scale task of mapping mycorrhizal association types of pre-European settlement USA and compare this to current maps at two finer-scale examples, California and the New York-New Jersey area. This study reveals how the majority of this land used to be covered by mycorrhizal vegetation, frequently containing multiple mycorrhizal types simultaneously. The comparisons with current maps effectively quantifies the degree of land loss, in terms of indigenous vegetation having been replaced with cropping systems of frequently non-native plants, or to developed areas such as cities and industrial areas. Such land loss has also brought about a major loss in the area of native mycorrhizal vegetation.

This paper is among those at the forefront of a rapidly developing research direction where mycorrhizal associations are integrated into vegetation science, macroecology and biogeography of plants, and the association itself. For example, the concept of plant community mycorrhization has been proposed and utilised to quantify how the degree and types of mycorrhizal associations are driven by vegetation composition and edaphic factors (Moora, 2014; Gerz et al., 2016). Furthermore, the developing understanding of mycorrhizal traits of plants (Hempel et al., 2013) is suggesting that these can and should be used as a type of plant functional trait in plant macroecological research (Menzel et al., 2016).

6. Conclusion

The papers of this special issue illustrate the diversity of mycorrhizas and mycorrhizal research in multiple ways. There are diverse types of mycorrhizal associations, and a dizzying number of ways in which the numerous species of host plants and fungi that have a mycorrhizal life styles interact with each other, and in turn influence the functioning of communities and ecosystems. While the understanding of these issues is continuously improving, this issue also displays a vibrant research front, and further goals to aim for.

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