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Caruso, T. (2018). Disentangling the factors shaping arbuscular mycorrhizal fungal communities across multiple spatial scales. *New Phytologist*, 220(4), 1248-1261. Advance online publication. <https://doi.org/10.1111/nph.15212>

Published in:
New Phytologist

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

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Type of contribution: Commentary

Disentangling the factors shaping Arbuscular Mycorrhizal Fungal communities across multiple spatial scales

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key words: AMF communities, multiple scales, spatial patterns, stochastic and deterministic determinants

Introduction

Soil biota is characterised by spatial patterns that range in scale from a few tens of micrometres to continental and global scales (Ettema & Wardle, 2002). The factors controlling these patterns across multiple spatial scales have been investigated extensively in the last years and there is now evidence that multiple factors contribute to these patterns but the relative importance of these factors is both scale and context dependent (Mummey & Rillig, 2008; Lindo & Winchester, 2009; Davison *et al.*, 2015; García de León *et al.*, 2016). Disentangling the relative roles of these factors and how these roles vary with spatial scales has thus become a central goal not only of soil biologists but also ecologists investigating aboveground-belowground linkages. Indeed, many groups of soil organisms are central to plant biology and ecology, including community dynamics (Bever *et al.*, 2010). Arbuscular mycorrhizal fungi (AMF) are particularly interesting in this context as they form a very important symbiotic association with plant roots. In the last 20 years, many studies have focused on the factors controlling AMF communities (Valyi *et al.*, 2016), including the reciprocal interactions that link AMF and plant communities (Van Der Heijden *et al.*, 2003; Zobel & Öpik, 2014). Yet, there are still significant gaps of knowledge about the relative roles of these factors and how these roles change across multiple scales. In this issue of *New Phytologist*, Rasmussen *et al.* (XXX) provide a novel and very detailed analysis of the multiscale patterns that characterise both root and soil AMF communities of *Plantago lanceolata*. This study is based on a hierarchical sampling design that finally bridges scales ranging from a few tens of cm up to tens of km. This study not only offers a novel quantification of AMF community structure across multiple spatial scales but also sheds light on the scale dependence of the roles of biotic and abiotic factors in structuring AMF communities. Very interestingly, Rasmussen *et al.* (XXX) also entered the role of non-AM root associated fungi into the equation, thus introducing a novel and underestimated level of complexity to the analysis of the factors that shape AMF communities.

High level of variation at small scales

The distribution of many groups of soil organisms, from bacteria and fungi (e.g., (Mummey & Rillig, 2008) to animals (Lindo & Winchester, 2009; Caruso *et al.*, 2012) is notoriously highly patterned already at very fine spatial scales. In general, the closer any two sampling sites are the more similar they will tend to be in terms of species co-occurrence and abundance of individual species. However, while Rasmussen *et al.* (XXX) confirm this result both for root and soil AMF communities they also highlight that variation at very small scale (i.e., among neighbourhood plants) was very high, indeed the highest across the scales analysed in their study, which ranged from the neighbourhood (30 cm) and subpopulation scale (10 m), to the population (10 km) and regional scale (30 km). The implication is that while AMF communities are very much spatially structured at the smallest scale, they are also least predictable in terms of taxonomic composition and diversity at this scale. This result is particularly intriguing because Rasmussen *et al.* (XXX) kept the focus plant constant across spatial scales, while most previous studies either sampled AMF associated to a mixture of plant species (Mummey & Rillig, 2008) or focused on one plant species but within a much shorter range of scales (Horn *et al.*, 2017). Which factors can explain both spatial structure and high variance at small spatial scales? Abiotic variables such as soil pH and the concentration of nutrients often show high variance at small scales and could potentially drive high variance of biotic communities at those small scales. Accordingly, many authors such as Lekberg *et al.* (2007) and Dumbrell *et al.* (2010) have typically found significant correlations between variables such as pH and AMF community variation across small to medium scales. However, a very interesting point made by Rasmussen *et al.* (XXX) is that different soil variables showed their highest level of variation at different scales, with variables such as pH that showed the highest variability at the smallest scales. Differences in the scale at which the highest variance is observed may thus point to the factors that play the major role in structuring AMF communities.

The role of biotic interactions

The reciprocal interactions linking plants and AMF communities have been shown to structure both sets of organisms, although the question of “who is driving whom” is complex to answer as the answer seems very dependent on the spatial and temporal scale of analysis (Zobel & Öpik, 2014; García de León *et al.*, 2016; Horn *et al.*, 2017). In general, both plant and AMF communities can structure each other depending on the successional stage at which the linkages between the two communities are considered. For example, many plant species establish earlier than their AMF symbionts during primary succession processes, which can make plants filter AMF colonisers. However, in long-term, stable communities regional differences in climate may cause non-mechanistic covariation (i.e., spurious correlation) between plants and AMF communities. Yet, at least at small scales, plant and AMF assemblages may even be weakly linked (Horn *et al.*, 2017). But what is the potential role of other groups of soil biota, especially other root symbionts? Rasmussen *et al.* (XXX) offer one important example of the analysis of covariation between AM and non-AM fungi in plant roots across spatial scales. The authors convincingly show that non-AM fungi, too, display higher variation at the smallest scales of analysis, correlating very well with AMF. Potentially, this covariation could be due to interactions between the two groups of fungi although it is too early to rule out the confounding effects of both abiotic factors and biotic interaction within each group of fungi and also between fungi and other soil organisms.

Stochasticity

A recurrent yet always surprising result of many studies is the small amount of variance usually explained by the measured abiotic and biotic factors, despite strong efforts made in terms of increasing the replication of observations, improving the structure of the sampling, and increasing the number of measured factors (Lekberg *et al.*, 2007; Dumbrell *et al.*, 2010). For example, Rasmussen *et al.* could overall account for not more than 20% of the total variance observed in their AMF communities, despite their sophisticated sampling design, the high number of replicates and measured variables, and their sampling around one single

focal plant species. Also, the 20% of accounted variance combines measured biotic and abiotic variables, and spatial structure not attributable to the measured biotic and abiotic variables. These results are definitely not the exception and while there can certainly be unmeasured abiotic and biotic factors to be entered into the equation, it is very possible that much of the unexplained variation is caused by stochastic processes. These processes could explain the relatively weak correlations often observed between the measured explanatory factors (e.g., pH and non-AM fungi) and the response variables (AMF communities in this case). The role of stochastic processes in structuring biological communities in general and AMF communities in particular, has gained increasing attention in the last 10 years, especially in relation to the very controversial neutral models of biodiversity (Lekberg *et al.*, 2007; Dumbrell *et al.*, 2010). In this context, it is very important not to confound the assumption of neutrality (i.e., all species demographically identical) with stochasticity itself. The assumption of neutrality is a very specific assumption, which defines a special class of stochastic models in community ecology (Vellend, 2010); stochastic processes are instead a general class of natural phenomena or, perhaps more correctly, of the human's way to model uncertainty in some natural phenomena. In the case of AMF, dispersal and colonization processes have the greatest potential to introduce various degrees of unpredictable and apparently random variation in community composition and taxa abundance (Lekberg *et al.*, 2011; Valyi *et al.*, 2016). This might be particularly relevant over subregional scales and when communities are sampled under very similar environmental conditions. As suggested by Rasmussen *et al.*, the fraction of unexplained variation due to stochastic processes may add up to the fractions of unexplained variation due to unmeasured abiotic and biotic factors. One of the future research challenges will then be estimating all these fractions and formulating experimental designs that may resolve the interaction between stochastic and deterministic processes.

In this context, the linkages between AMF communities in root and soil AMF communities may play a key role. The question of which of either soil or root AMF communities is more diverse and of whether or not the two communities significantly differ in terms of taxonomic

composition has puzzled AMF specialists for many years and contrasting evidence seem to suggest that the various possible scenarios may all occur but each under different environmental conditions and at different spatial and temporal scales. Rasmussen *et al.* add an intriguing point to the debate: taxonomically, soil and root communities can have very similar structure in terms of relative abundances of genera and shared dominant OTUs. Yet, root communities can have higher richness. The interaction between the stochastic and deterministic processes that determine the AMF colonization of roots may play a major role in determining the differences between the root and soil AMF communities. A future and urgent challenge will thus be adding this further level of complexity to the analysis of the processes structuring AMF community. Resolving this challenge will likely require a standardization of sampling methodologies both in terms of experimental design (e.g., spatial structure of the sampling strategy) and quantification of AMF biota (e.g., sequencing depth for root and soil).

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