OPEN

The ISME Journal (2016) 10, 2341–2351

www.nature.com/ismej

MINI REVIEW

Community assembly and coexistence in communities of arbuscular mycorrhizal fungi

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Arbuscular mycorrhizal fungi are asexual, obligately symbiotic fungi with unique morphology and genomic structure, which occupy a dual niche, that is, the soil and the host root. Consequently, the direct adoption of models for community assembly developed for other organism groups is not evident. In this paper we adapted modern coexistence and assembly theory to arbuscular mycorrhizal fungi. We review research on the elements of community assembly and coexistence of arbuscular mycorrhizal fungi, highlighting recent studies using molecular methods. By addressing several points from the individual to the community level where the application of modern community ecology terms runs into problems when arbuscular mycorrhizal fungi are concerned, we aim to account for these special circumstances from a mycocentric point of view. We suggest that hierarchical spatial structure of arbuscular mycorrhizal fungal communities should be explicitly taken into account in future studies. The conceptual framework we develop here for arbuscular mycorrhizal fungi is also adaptable for other host-associated microbial communities.
The ISME Journal (2016) **10,** 2341–2351; doi:10.1038/ismej.2016.46; published online 19 April 2016

Introduction: applying models of community assembly and contemporary coexistence theory to communities of arbuscular mycorrhizal fungi: knowledge gaps and difficulties

How communities assemble and which species can coexist in the same locale has been a central question of ecology. The recent advancement of high-throughput molecular barcoding methods has enabled researchers to obtain information on the composition and structure of natural microbial communities more easily than ever. This is especially important for organisms that are difficult to culture, such as arbuscular mycorrhizal (AM) fungi, which are obligate symbionts of plants where they form multispecies symbiont communities in the same root. Given the growing number of molecular studies in the field of AM fungal community research, it is timely to review the progress on understanding the processes that underlie AM fungal community assembly, and highlight the knowledge gaps.

The theoretical framework of community assembly and coexistence (HilleRisLambers *et al.*, 2012) combines a classic filter model of community assembly with modern coexistence theory (Chesson, 2000). The filter model describes a regional pool of species from which the members of local communities are selected by passing through environmental and biotic filters. Modern coexistence theory (Chesson, 2000) addresses interactions on the local scale, which arise from niche differences and fitness similarities. The combined approach therefore acknowledges factors on a wide spatiotemporal scale. Regional and local processes are connected by the neutral process of dispersal. The filter model is further nuanced by taking into account feedbacks, when organisms are not only influenced by but also have an impact on their environmental and biotic filters (Figure 1).

AM fungi are a monophyletic group (phylum Glomeromycota) of asexual, obligately symbiotic fungi with a unique combination of traits regarding morphology, genomic structure and ecology. Within their coenocytic mycelia and spores, multiple, potentially genetically divergent nuclei coexist, making it difficult to delineate an individual even with molecular methods (Table 1). Through intraradical and extraradical mycelia, they occupy a dual niche, the plant root and soil. Both the soil environment and plant root can be described according to a simple filter model as species filters preventing certain AM fungal species from entering the local community. However, the simple filter analogy ends when taking into account that host plants and soil do not remain unchanged during community assembly: AM fungi interact with their hosts through hormonal crosstalk and actively shape soil as ecosystem engineers (See section: '*Feedbacks: AM fungi as ecosystem engineers*'). Taking into account these

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Received 1 September 2015; revised 15 February 2016; accepted 17 February 2016; published online 19 April 2016

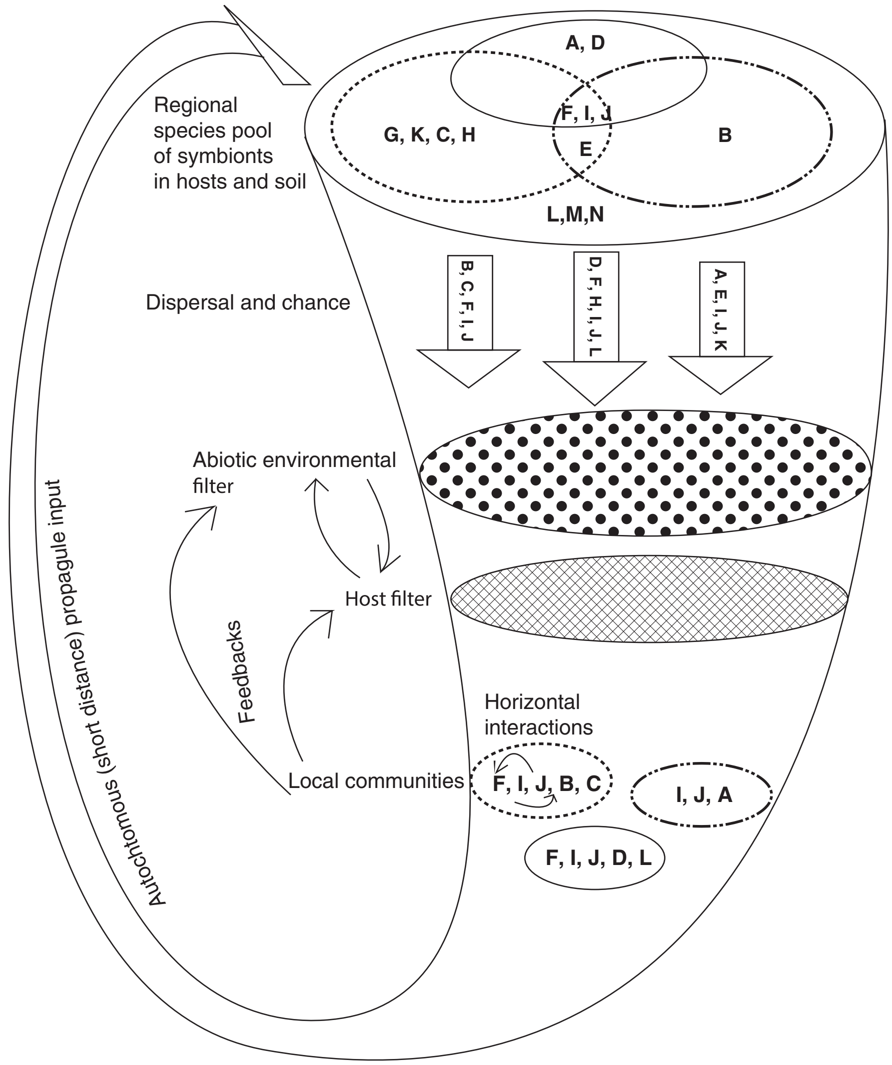

Figure 1 Applying the combination of a filter model of community assembly and neutral processes for AM fungi. The regional pool of AM fungi consists of species present in the soil and in the roots of the host community. Through local or long-distance dispersal and chance, species reach local habitats. The environmental filter prevents species whose environmental tolerances do not overlap with local conditions from entering the community. The host filter allows colonization only for compatible fungal partners, thus further removing species. The local community reflects the cumulative effects of these processes, and in turn influences them through feedbacks. Horizontal interactions within the symbiotic community and with other non-host species also affect local communities. Local communities in turn contribute to the regional species pools with autochtonous propagule input. The capital letters refer to different AM fungal species. Ellipses with different lines depict different root system communities. Details of the depicted community assembly and coexistence model elements can be found in the section '*Factors affecting AM fungal community assembly: review of the elements of the proposed model*' in the main text.

developmental, genetic and ecological angles, the direct adoption of models for community assembly developed for other organism groups is not evident. There are several points from the individual to the community level where the application of modern community ecology terms runs into problems when AM fungi are concerned (Table 1). Especially in the area of coexistence, even for the definitions of such fundamental concepts as ‘fitness’ further research and discussion are needed (Table 2).

Here we introduce the elements of a community assembly and coexistence model by highlighting recent research on AM fungal communities. As examples for each element, we included studies that used DNA-based methods (preferentially, high-throughput sequencing approaches) to investigate AM fungal communities.

Factors affecting AM fungal community assembly: review of the elements of the proposed model

Regional pool

AM fungi have species pools with distinct composition according to paleocontinents, although endemic species are rare (Kivlin *et al.*, 2011; Davison *et al.*, 2015). Regionally, observed AM fungal communities

Table 1 Fundamental questions in defining levels of biological organization for AM fungi

Level of biological organisation	*General definition*	*Problem with usage for AM fungi*	*Possible solutions*
Individual	In modular organisms, an individual can be defined: • as a physically continuous unit, which is separated from other such units (ramet) • a unit with uniform genetic composition (genet)	In AM fungi, these two definitions do not delineate the same parts of the mycelium (Rosendahl, 2008): • genetically different AM fungi are able to anastomose with each other (Chagnon, 2014) and might form a continuous mycelium where nuclei of different genetic compositions mingle (Young, 2009) • a genetically uniform mycelium might be physically disrupted • because of asexual reproduction with no recombination, different mycelia with the same genetic composition can be found in large geographical distance from each other • 'ramet' and 'genet' are used by some researchers; however, many use the terms 'clone', 'strain' and 'isolate' as with other microbes to grasp different aspects of the concept of an individual	• DNA profiling of individuals using mitochondrial markers, because, in contrast to nuclear DNA, the mitochondrial genome appears to be genetically identical within mycelia (de la Providencia *et al*., 2013; Daubois *et al*., 2016)
Species	Some commonly applied species concepts for fungi are (Moore *et al*., 2011): • morphological: based on morphological similarity • biological: based on reproductive isolation • phylogenetic: defining OTUs based on genetic similarity	• Morphological: many AM fungal species are unculturable and their appearance in roots varies with the host • Biological: no evidence of sexual reproduction, so mating tests are not possible • Phylogenetic: It is not clear what level, if any, of genetic difference is a suitable proxy for species or other levels of biologically interacting units (Hao *et al*., 2011; Caruso *et al*., 2012b; Powell, 2012)	• Morphological: traditional taxonomy of AM fungal morphotypes is based on the characteristics of spores • phylogenetic: – Fixed and named OTUs are available for the sake of comparability between environmental studies, based on the small subunit of the ribosomal DNA (Öpik *et al*., 2010) – Efforts are made to create a unified sequence-based species delimitation of Glomeromycota using multiple loci (Öpik *et al*., 2014)
Community	Species with similar ecology that coexist in the same spatial region (Chesson, 2000). Definitions often include that community members must be able to interact (for example, Whittaker, 1975)	At which spatial scale should the AM fungal community be defined?	Adapting a spatially explicit, hierarchical community system from parasitology (Figure 2, see also section '*Scale dependency: different assembly rules for different spatial scales? An analogy borrowed from parasite communities*' in the main text): • AM fungi in a root fragment • infracommunity: AM fungi in an entire root system of one host • component community: AM fungi in the root systems of a population of one host species • compound community: AM fungi in the root systems of the host community (mixed root samples from a sampling site)
Metacommunity	Metacommunities are spatially divided species assemblages, where dispersal among communities is limited (Morin, 2011)	The assemblage of AM fungal communities living in the root systems of a plant community cannot be easily described by the metacommunity theory: • instead of only dispersing between hosts by propagules, AM fungi in different hosts might interact or even be physically continuous with AM fungi living in other root systems, forming CMNs (Selosse *et al*., 2006), which are large, interconnected networks of fungal hyphae that are simultaneously connecting multiple hosts • hosts are not passive islands: – AM fungi can preferentially allocate nutrients to high-quality hosts connected to the same CMN (Fellbaum *et al*., 2014) and CMNs can provide means of infochemical transport between connected plants (Barto *et al*., 2011) – AM fungi can modify the fitness of their hosts depending on their identity. Furthermore, responsiveness of hosts to AM fungal colonization can change over time after the initial colonization (Veresoglou *et al*., 2012; Mihaljevic, 2012a, b)	Application of metacommunity theory would require modifications

Abbreviations: AM, arbuscular mycorrhizal; CMN, common mycorrhizal network; OTU, operational taxonomic unit.

are spatially heterogenous, but temporally stable, suggesting a fairly constant soil species pool from which mycorrhizae form during the season (Davison *et al.*, 2012).

Dispersal and chance (neutral processes)

Propagules and vectors of dispersal in AM fungi. AM fungi disperse by autochthonous (local mycelium spread) and allochthonous propagules (spores and other inoculum, such as hyphal fragments or colonized root fragments from outside), with the allochthonous propagules being less important locally (Jumpponen and Egerton-Warburton, 2005). AM fungi often have large spores, and many species are distributed by zoochory (for example, through the guts of rats (Janos *et al.*, 1995), earthworms (Shapiro *et al.*, 1993) and collembolans (Klironomos and Moutoglis, 1999) or on the hooves of bison (Lekberg *et al.*, 2011)) as opposed to wind, where their spores are detected rarely (Egan *et al.*, 2014). Thus, AM fungal species are mostly limited to short-distance dispersal. However, over long timespans, these limited dispersal capabilities allow for a surprisingly efficient spread of taxa (Davison *et al.*, 2015).

Spatial community structure, dispersal limitation and other stochastic processes. AM fungal communities are spatially structured, patchily distributed even in relatively homogenous local environments (Rosendahl and Stukenbrock, 2004; Mummey and Rillig, 2008), which suggests that there are other processes beyond environmental filtering that contribute to the structure of AM fungal communities, for example, dispersal limitation. The relative importance of dispersal to environmental filtering is scale-dependent and varies (soil type and dispersal ability, Lekberg *et al.*, 2007; soil pH, C/N ratio, phosphorus and dispersal, Dumbrell *et al.*, 2010a; soil temperature, plant biomes and dispersal, Kivlin *et al.*, 2011). Dispersal and other neutral processes thus exhibit an effect size spectrum that can be completely masked by extreme environmental heterogeneity or anthropogenic disturbance, resulting in communities more dissimilar than expected under the assumptions of neutral theory. On the other hand, stochastic effects are also limited under very homogeneous environmental conditions because of niche effects (Caruso *et al.*, 2012a).

Environmental filter

Niche partitioning along environmental gradients. The assembly process and the coexistence of AM fungi are influenced by various soil environmental variables, such as pH, soil type, soil chemistry and nutrient availability. As nutrient transport is a function of AM fungi, the effect of nutrient availability is well studied (reviewed in Johnson, 2010). The filtering role of the environment, when some species from the regional pool are not present under certain soil conditions, was shown in fertilizer addition experiments: AM fungal phylotype diversity decreased with increasing N and P availability and some AM fungi were only found in specific soil nutrient conditions (for example, Liu *et al.*, 2012; Camenzind *et al.*, 2014; Liu *et al.*, 2015).

Seasonality. AM fungi show temporal niche partitioning over the course of the year. Previously rare types might replace the dominant species (Husband *et al.*, 2002). As possible explanations for this shift, both changing environment, for example, changes in temperature and sunshine hours (which influence the soil carbon pool, Dumbrell *et al.*, 2011), and the seasonal cycle of the plant community and phenology were suggested.

Disturbance. Increasing agricultural land-use intensity selectively removes rare AM fungal species from the local community (Helgason *et al.*, 1998; Verbruggen *et al.*, 2012). Heavy anthropogenic disturbance, such as plowing, tillage and fungicide treatment, can lower the number of AM fungal species, abundance and root colonization while favoring generalist species (Helgason *et al.*, 1998; Hijri *et al.*, 2006; Helgason *et al.*, 2007; Schnoor *et al.*, 2011). However, disturbance does not always shift communities in a predictable way (Lekberg *et al.*, 2012) probably because of the dominance of stochastic effects (Caruso *et al.*, 2012a).

Host filter

One of the particular features of AM fungal community assembly is the importance of the host filter compared with free-living or facultatively symbiotic organisms. Plants restrict AM fungal diversity in roots (Johnson *et al.*, 2004) and they also differentially influence sporulation (Eom *et al.*, 2000). Given the obligatory symbiotic AM fungal lifestyle, the existence of host effects could be obvious. The non-evident detail in the host–AM fungal relationship is the apparent lack of species-level specificity (there are many fewer AM fungal species than plant species, even though most land plants are mycorrhizal). As an explanation, it was proposed that being able to colonize and to be colonized by a wider range of partners has an evolutionary benefit, and that environmental conditions affect the ability of plants to differentially reward their symbionts (reviewed in Walder and van der Heijden, 2015). In the field, different plant species, and even plants of the same species at different growth stages, associate with different fungal communities from the same soil (Gollotte *et al.*, 2004; Sýkorová *et al.*, 2007; Gosling *et al.*, 2013) and some AM fungi do not colonize certain plants (Helgason *et al.*, 2002). AM fungi differ regarding how beneficial they are for hosts (Helgason *et al.*, 2007), and plants are able to reward better fungal partners with photosynthates (Bever *et al.*, 2009; Kiers *et al.*, 2011). The solution might be that

Table 2 Problems and solution attempts in applying community ecology terms to AM fungi

Community ecology term	*Problems in using it in AM fungal community ecology*	*Current solution attempts and their issues*
Fitness	The definition of fitness in other organisms usually includes a measure of reproduction. • As AM fungi are asexual organisms, how can their fitness be defined? • It is difficult to use a proxy for AM fungal fitness, which could be used to compare species, as: (1) higher propagule abundance does not necessarily translate to higher colonization (2) there are significant allocation differences among species in growth of spores versus hyphal network (Veresoglou and Halley, 2012) • AM fungal fitness always depends on plant carbon, as they do not have independent ways to take up carbon (Johnson, 2010)	• Spore production and root colonization rates are possible fitness measures • Marker gene copy numbers can be used as a proxy of root colonization (Thonar *et al*., 2014). Distinguishing some AM fungal species in co-colonized roots is now possible with species-specific quantitative real-time PCR
Traits	How to study AM fungal traits?	• Traits in culture: traits are assigned to strains and might not be representative of a species • Transcriptomes of a single species: the study of the transcriptomes of species (Tisserant *et al*., 2012) might explain perceived functional redundancy (Peay *et al*., 2008) and provide mechanical understanding of community assembly, but it suffers from the same problem • Metatranscriptomes: solving the annotation problem in the emerging field of metatranscriptomics might enable us to study traits in field communities
Niche	Dual niche of AM fungi in root and soil	• AM fungi are obligate symbionts, but not only are they required to colonize a root system to complete their life cycle, but also to forage in the soil for nutrients and water • Thus, they are affected by factors both within and outside the root system at the same time • The composition of AM fungal communities is different in the two compartments (Hempel *et al*., 2007), and it is likely that forces governing soil and root communities are different (Liu *et al*., 2012) • AM fungal species differ in functional traits regarding spatial niches (for example, to what extent do they colonize roots or soil), and these traits are also conserved (Hart and Reader, 2002; Powell *et al*., 2009)
Bipartite networks	How does the network theory describe host–AM fungal interactions (Chagnon *et al*., 2012)?	• AM fungal–plant networks regularly show nestedness (species interact with a subset of the species generalists interact with) and modularity (species tend to group into modules in which interactions are more frequent than with the rest of the community; Öpik and Moora, 2012; Verbruggen *et al*., 2012) • These network characteristics may derive from overdominance of the founder AM fungus (Dumbrell *et al*., 2010b), habitat heterogeneity, specific selectivity in plant–AM fungal associations, plant–AM fungal overlapped phenology or AM fungal competition within the root (Montesinos-Navarro *et al*., 2012) • However, in order to correctly apply network theory to AM fungal–plant interactions, basic assumptions need to be verified, that is, detected co-occurence must imply interactions (Caruso *et al*., 2012b)

Abbreviations: AM, arbuscular mycorrhizal; PCR, polymerase chain reaction.

host specificity does not happen at the species level, but on an ecological level, where generalist AM fungi interact with generalist plants while specialists tend to occur in the roots of specialist plants (Öpik *et al*., 2010; Davison *et al*., 2011). Furthermore, pairings of hosts and symbionts with similar life history strategies (competitive, stress tolerant, ruderal, as described for AM fungi in Chagnon *et al*., 2013) are likely more beneficial. The functional traits defining these strategies are often conserved at a higher taxonomic level (Maherali and Klironomos, 2007; Chagnon *et al*., 2013). Not only the host itself but also neighboring plants (Hausmann and Hawkes, 2009) and plant species richness (Burrows and Pfleger, 2002; Engelmoer and Kiers, 2015) influence fungal communities. In addition, AM fungal preference regarding hosts also exists (Davison *et al*., 2011).

Non-host biotic interactions and feedbacks

Horizontal interactions between members of local AM fungal communities. Past work has found intense competition for root space (Cano and Bago, 2005; Engelmoer *et al.*, 2014) and even competitive exclusion (Hepper *et al.*, 1988). As opposed to root colonization, the ability of AM fungal species to colonize soil did not influence coexistence (Maherali and Klironomos, 2012). Phylogenetic overdispersion promotes coexistence: communities of more distantly related and functionally different species showed higher realized species richness (Maherali and Klironomos, 2007). Conserved differences in other functional traits, such as timing of spore production and hyphal growth rate, metabolism of photosynthates, P and N uptake, might alleviate competition as well.

Despite the potential importance for commercial use of fungal inocula, the effect of arrival order in AM fungi is not well understood. Priority effects were shown (Mummey *et al.*, 2009); however, it was recently observed that the resident AM fungi did not suffer from reduced growth despite being invaded, which makes competition for space an unlikely explanation, and suggesting downregulation by the host instead (Werner and Kiers, 2015).

Interactions with other non-host organisms. Negative interactions with consumers (fungal grazers), pathogens and parasites could reduce competition between AM fungi. However, collembola feeding on AM fungi had no effect on the community composition (Gange, 2000), and parasitism has not yet been conclusively shown to exist in AM fungi (Purin and Rillig, 2008). Either these interactions are really not important for AM fungal communities or we are limited by data.

AM fungi harbor bacteria associated with their spores. These bacteria promote hyphal growth and stimulate nutrient biodynamics. They might facilitate not only the fungus, but the whole mycorrhizal system by contributing to the suppression of soil-borne plant pathogens and by adding nitrogen fixation to the benefits of the plant (Cruz and Ishii, 2011).

Feedbacks: AM fungi as ecosystem engineers. AM fungi significantly modify their habitat both in the soil and in the plant in a way that influences their own communities. In the soil they increase soil aggregation and the water stability of the aggregates by a variety of mechanisms, including hyphal enmeshment (Rillig *et al.*, 2015). Greater particle size and pore space may in turn benefit hyphal growth (Rillig and Steinberg, 2002).

They affect plant diversity and composition by improving the nutrient status of their host plants and by facilitating their hosts, which was shown to induce shifts in plant communities (van der Heijden *et al.*, 1998). To harness this effect, enhancing natural AM fungal communities is suggested as an environmentally friendly weed-control option in agricultural ecosystems (Cameron, 2010). On the other hand, plant community composition also has an effect on AM fungal communities, completing the feedback loop.

Relative importance of different elements: possible explanations for the idiosyncratic response of AM fungi to biotic and abiotic variables

Despite the considerable literature that exists on the host, abiotic environmental and neutral factors influencing AM fungal community composition, there is no consensus on their relative importance. AM fungi have an idiosyncratic response to these variables. We propose two hypotheses to explain this pattern.

'Law of the minimum': an idea from plant nutrition. In agricultural science, the 'law of the minimum' is an idea that the scarcest essential nutrient (the most limiting factor) is the most important in determining plant growth (Gorban *et al.*, 2011). Similarly, but stepping away from only thinking about resources, the relative importance of assembly factors would depend on the most restrictive component, and the most limiting factor would explain the most variability. Under non-filtering environmental conditions, in an abiotically homogenous sampling area, host effects would be relatively more important. A strong environmental gradient that includes harsh conditions unsuitable for certain species would result in environmental filtering as the dominant structuring force.

Scale dependency: different assembly rules for different spatial scales? An analogy borrowed from parasite communities. Studies on AM fungal communities vary strongly in the spatial scale being addressed. Definitions range from AM fungi found in a root piece through an entire root system to a mixed root sample of an entire site. As different assembly factors act on different scales, explicitly considering the spatial structure of AM fungal communities could lead to a synthesis between contrasting responses to assembly factors (for example, host versus abiotic environmental filter). Parasitology defines a hierarchical, host-based, scale-dependent community system (Figure 2 and Table 1). In infra- and compound communities of fleas, which also have varying levels of host specificity, the relative importance of environmental and host effects depends on the spatial scale (Linardi and Krasnov, 2013; Krasnov *et al.*, 2015). AM fungal communities have a similar host-based hierarchical spatial structure (Figure 2); therefore, it is a compelling idea that the relative importance of assembly factors depends on the spatial scale in AM fungi too. Maherali and Klironomos (2012) hypothesized that subplot-scale interactions (infracommunity) such as competition could determine coexistence, whereas the AM fungal composition of a whole site (compound community) would mostly depend on niche requirements or climate (environmental filter). Consequently, AM fungal communities are found to show phylogenetic

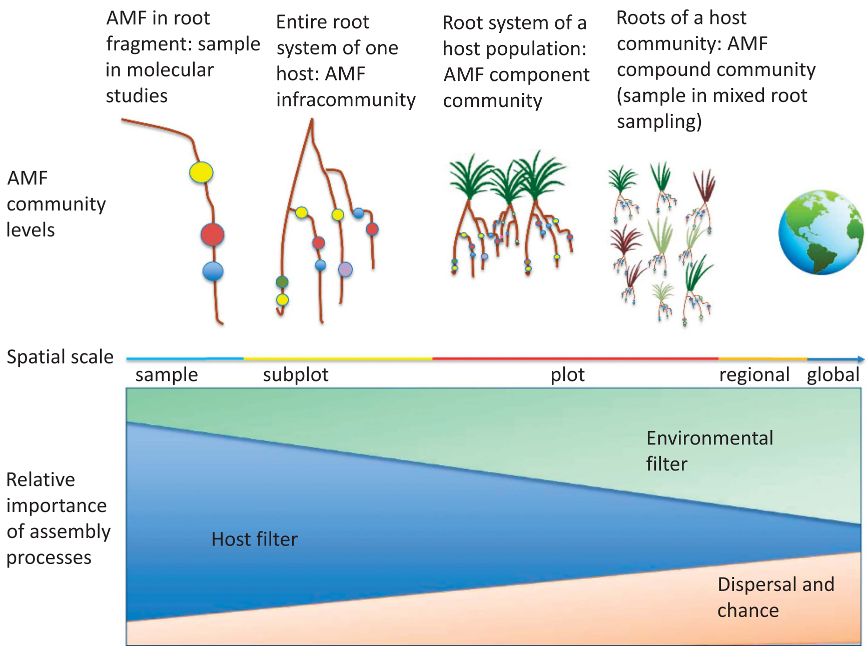

Figure 2 Hierarchical scale-dependent community system in AM fungi. At a given spatial (or temporal) scale, multiple processes influence the assembly of AM fungal communities. Relative importance of assembly processes changes with spatial scale, causing idiosyncrasy in response to different assembly factors, when the hierarchical spatial structure is not explicitly considered.

clustering within study sites (Kivlin *et al*., 2011), with sometimes negligible effects of the environment (Horn *et al*., 2014), which might indicate facilitation between species. At a global scale, the AM fungal community composition was shown to be best predicted by spatial distance, edaphic and climatic factors, and plant community type (Kivlin *et al*., 2011; Davison *et al.*, 2015). To sum up, the scale dependency of the relative importance of the elements of community assembly and coexistence is well established in many organisms; however, explicit consideration of spatial scale in AM fungal community studies is still rare. An example of how the relative importance of the assembly processes might change with spatial scales is shown in Figure 2.

Conclusion: community ecology from the viewpoint of a microbial symbiont

We presented a conceptual framework of community assembly and coexistence adapted to a microbial symbiont group with a unique combination of characteristics. The importance of factors influencing obligate symbionts differs from those affecting free-living organisms, or even facultative symbionts (Linardi and Krasnov, 2013). The host–AM fungal relationship, similarly to parasites, exhibits a hierarchical spatial structure, which should be explicitly incorporated into future studies, to enable the study of the scale dependency of the relative importance of elements of community assembly. Adapting a symbiont-centered point of view in addition to considering how the host community is affected would help to fill the knowledge gaps of coexistence research, especially in the field of non-host interactions.

Outlook: how further research on AM fungal communities could advance the field of community assembly and coexistence theory

Owing to the advance of high-throughput molecular methods, researchers gained insight into the communities of specialized organisms, for example, the AM fungal communities in plant roots. With the number of AM fungal community studies rising, it is now possible to start to piece together the mechanisms influencing community assembly and coexistence. By considering the unique combination of characteristics in genetic makeup, physiology, niche and dispersal of AM fungi, and highlighting problems in applying community ecology concepts stemming from these, we are getting closer to adapting community assembly and coexistence models to them.

Taking levels of community organization related to the host into account (infracommunities, component communities and compound communities, see Figure 2) can help reconcile contrasting results regarding the relative importance of assembly factors.

In AM fungi, where the effect of the host filter is so significant, non-host biotic interactions, although they might not be able to act as a filter in community assembly, are still influencing community structure, and future studies in this currently neglected field might reveal more interesting relations.

Examining different assembly and coexistence factors in a multitude of specialized microbial groups would help advance the field of community ecology by increasing the external validity of its models and theories. Although it is important to transfer concepts from general ecology, it is critical that these concepts be carefully evaluated before application (Table 1): two examples are the application of metacommunity concepts to symbiotic systems (Veresoglou *et al.*, 2012) and the use of network theory in mycorrhizal ecology (Caruso *et al.*, 2012b); in both cases it is important to verify the validity of assumptions lest analyses be misleading. Emerging concepts in community ecology, like metrics for quantifying intransitive competition (Soliveres *et al.*, 2015) or community coalescence (Rillig *et al.*, 2015), will require similar validation to apply them to specific microbial communities. Doing so can lead to new hypotheses in the AM fungal and broader community ecology, as in applying community phylogenetics (Webb *et al.*, 2002 ; Vamosi *et al*, 2009) to AM fungi: after carefully proving that AM fungal traits related to spatial niche use are conserved at a higher taxonomic level (Maherali and Klironomos, 2007), this was used to generate hypotheses and a theoretical framework on the coupling of plant and AM fungal life history strategies (Chagnon *et al.*, 2013).

Answers to the questions of community assembly and coexistence in AM fungi are increasingly required in order to more successfully manage AM fungi for application. Community composition influences ecosystem services, which is true also for AM fungi (van der Heijden *et al.*, 1998). Better understanding of AM fungal communities could be a powerful tool in mitigating the effects of global change, for example, in agriculture and habitat restoration.

Conflict of Interest

The authors declare no conflict of interest.

Acknowledgements

We thank the editor, two reviewers and W Zheng for their valuable comments. MCR thanks BMBF for funding through the BonaRes initiative (INPLAMINT). SH and KV thank DFG (grant number HE 6183/1-1). UM thanks DRS HONORS Fellowship programme of Freie Universität Berlin.

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