



## *Tansley review*

# Ectomycorrhizal fungi and interspecific competition: species interactions, community structure, coexistence mechanisms, and future research directions

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### Summary

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The field of ectomycorrhizal fungal (EMF) ecology has largely developed outside the ecological mainstream, owing in large part to the challenges in studying the structure and dynamics of EMF communities. With advances in molecular identification and other research techniques, however, there has been growing interest among mycologists and ecologists in understanding how different ecological factors affect EMF community structure and diversity. While factors such as soil chemistry and host specificity have long been considered important, an increasing number of laboratory and field studies have documented that interspecific competition also has a major impact on EMF species interactions and may significantly influence EMF community structure. In this review, I examine the progress that has been made in understanding the nature of EMF competition. Currently, there are four conclusions that can be drawn: negative competitive effects are rarely reciprocal; competitive outcomes are environmentally context-dependent; field distributions often reflect competitive interactions; and timing of colonization influences competitive success. In addition, I highlight recent studies documenting links between competitive coexistence and EMF community structure, including checkerboard distributions, lottery models, storage effects, and colonization–

competition tradeoffs. Finally, I discuss several aspects of EMF competition needing further investigation and some newer methods with which to address them.

## I. Introduction

Since at least the time of Darwin, ecologists have considered competition to be one of the dominant forces affecting the way species interact. A wide range of studies have found that competition is common in many species interactions (Connell, 1983; Schoener, 1983; Goldberg & Barton, 1992; Denno *et al.*, 1995; Hibbing *et al.*, 2009) and that it can have significant effects on the structure of entire communities (Keddy, 2001; and references therein). While a more pluralistic view of the factors structuring ecological communities has arisen in recent years (Stachowicz, 2001; Kaplan & Denno, 2007; Cavender-Bares *et al.*, 2009), the study of competition and its effects on both individual species and communities remain a core aspect of ecological theory and practice (Townsend *et al.*, 2008).

Although largely unrecognized outside the mycological community, the study of competition among fungi has a considerable history dating back to the 1940s (Lockwood, 1981; Wicklow, 1992; Widden, 1997). Much of the early work examined intraspecific and interspecific competition among crop pathogens such as *Fusarium*, *Phytophthora* and *Puccinia* (Garrett, 1956, 1970). Following those studies, research focused heavily on the effects of competition in saprotrophic fungal communities (Shearer, 1995; Boddy, 2000). More recently, competitive dynamics have also begun to be investigated in mutualistic fungal guilds, such as arbuscular mycorrhizal fungi (AMF) (Lekberg *et al.*, 2007; Smith & Read 2008, pp. 74–76; Bennett & Bever, 2009).

While the importance of competition has been recognized for many fungal groups, its role in ectomycorrhizal fungal (EMF) interactions has developed more slowly. This is surprising given the widespread occurrence and ecological significance of this fungal guild (Smith & Read, 2008). It has been well documented that different EMF species have varying effects on both host plant growth as well as rates of soil nutrient cycling (e.g. Courty *et al.*, 2005; Nara, 2006), so determining the effects of competition seems paramount to a full understanding of the ecological function and diversity of EMF communities.

There appear to be two main reasons for the delay in studying EMF competition. The first is technical and relates to the challenges associated with manipulating EMF species composition. Because most EMF species do not grow well in culture or have spores that readily germinate in the presence of host roots (Ishida *et al.*, 2008), creating the single and multispecies treatments needed to assess competition in

laboratory settings has been more difficult than for other groups of fungi. Similar challenges are present in field settings because EMF species grow cryptically belowground and often lack species-distinguishing features in their root-tip and hyphal morphologies. As a result, EMF communities cannot easily be selectively manipulated like those of plants, animals, and less cryptic organisms. The second reason why competition has received less attention appears to be related to the mutualistic nature of EMF symbiosis. Because EMF-host plant interactions are largely positive (Smith & Read, 2008), there has been a strong research emphasis on positive interactions ('complementarity') among EMF species in promoting host plant growth. However, this focus has overlooked the fact that these fungi are no different from organisms that compete among themselves when resources are limited. Given that both the host and soil resources required for EMF species are finite, interspecific competitive interactions should not be surprising. Indeed, similar types of interguild competition have been well documented in other plant-related mutualisms (Palmer *et al.*, 2003; Blanco *et al.*, 2010).

Despite these barriers, a rapidly growing number of studies have begun to investigate the dynamics of EMF competition. The goal of this review to provide a synopsis of what is currently known about the topic, both in terms of the way EMF species compete as well as the effects of competition on EMF community structure. Bruns (1995) provided much of the intellectual foundation for the latter and this review will focus primarily on the data that has emerged since then. There are a number of studies suggesting that EMF communities are influenced by competition in similar ways to those of more well-studied organisms (Townsend *et al.*, 2008). However, the inherent challenges associated with studying EMF communities have made documenting competitive effects in the field and at the community level difficult. Therefore, caution should be exercised in generalizing about the importance of competition. As will be discussed later, it is likely that factors that play a structuring role in EMF communities, of which competition is only one, are not mutually exclusive and their relative importance changes at different spatial and temporal scales. As the study of EMF competition is still in a nascent phase, this review also highlights a number of untested research questions. Their answers will be greatly facilitated by the use of new approaches and techniques. Fortunately, many of both have been developed in recent years and the increasing collaboration between EMF ecologists and researchers from

other fields suggest the study of EMF competition is primed for further study.

## II. Definitions and terminology

Ecologists and mycologists have both proposed a wide range of definitions for competition (Tuininga, 2005). Many focus on the outcome of the interaction, while others focus more on the process. For EMF competition, the use of process-based definitions is difficult because it is still largely unknown how exactly resources are traded with their host plants. As stated by Bruns (1995), the actual host resource for which EMF species compete is carbon (they, of course, also compete for nutrient resources in the soil), but this kind of competition is typically assessed by counting the number of root tips occupied by different species with the assumption that more root tips equals more carbon. Using root tip counts as a proxy would work if all EMF species exchanged carbon with all hosts at the same ratio, but this is highly unlikely to be the case (Bidartondo *et al.*, 2001). Because of this complication, I will use an outcome-based definition of competition here: a decrease in the growth of one EMF species in the presence of another EMF species. Note this definition stresses a comparison between the performance of a species alone vs in the presence of other species. This means that field observations of EMF abundance and rarity can suggest that competition may be occurring, but ultimately experimental manipulations are necessary. An outcome-based definition is also needed because EMF competition involves both direct species interactions and depletion of common resources (strict resource-based definitions only address the latter). Unfortunately, this kind of definition has the disadvantage of being more phenomenological than mechanistic (Chesson, 2000), so *a priori* predictions about competitive exclusion and coexistence are not possible. Furthermore, outcome-based definitions have the difficulty that identical outcomes can be caused by different processes. For example, plant ecologists often differentiate the negative effects caused by allelopathy from those caused by competition (Williamson, 1990), although both lead to same outcome. While careful experimentation can separate the effects of chemical deterrence vs resource depletion, at least for plants, there is good evidence that these two processes are positively correlated in nature and are likely synergistic (Inderjit & Del Moral, 1997). I therefore caution the reader to remain vigilant about the possibility of alternative explanations aside from competition in the studies discussed later.

The majority of EMF studies have focused on competition for plant root space because it is the site of nutrient exchange and EMF species require host carbon to survive (Smith & Read, 2008). However, mycelial competition for nutrients and water in soil is equally important and has received increasing attention as methods for studying this

part of the EMF symbiosis have advanced (Leake *et al.*, 2004). For both root tip and mycelial competition, there are two ways that EMF species negatively affect their competitors. The first is through exploitation competition (also known as pre-emptive competition), which involves an ability to more rapidly colonize root tips or acquire soil nutrients. In this type of competition, one species consumes resources to the detriment of their competitors, but there is no direct interaction among species. The second is interference competition (also known as direct competition), which involves direct antagonistic interactions among competitors through either behavioral or chemical means. Examples of interference competition include the takeover of occupied root tips by a different species or the production of antifungal compounds to prevent other EMF species from growing in the same location. (The latter could be interpreted as exploitative competition, but the fact that the compound directly harms the targeted competitor means that the competing species are interacting more than just indirectly through a common resource).

I believe it is also useful to differentiate the two main ways that competition has been studied. As stated by Bengtsson *et al.* (1994), 'one is to examine proximate mechanisms of competition, by focusing on the acquisition and use of resources and on the traits that determine competitive ability. The other is to focus on the results of competition, that is to analyze community structure and the maintenance of diversity'. For EMF, the focus has been on the former, although there is growing interest in determining the extent to which competition influences community-level species distributions (Koide *et al.*, 2005; Peay *et al.*, 2007). In addition, ecologists have made a distinction between competitive response and competitive effect (Goldberg, 1990). Competitive effect refers to the ability to suppress resource levels for other species while competitive response is the ability to tolerate suppression of low resource levels. Although these terms have helped clarify the ways in which plants compete (Bengtsson *et al.*, 1994), they have yet to be applied to EMF competition. I note them here because the theoretical framework laid out by Goldberg (1990) is well suited for EMF competitive interactions (the intermediary in this case being the plant host) and these terms emphasize the importance of studying competition across environmental gradients. Currently, there have been no direct studies of EMF competition across any environmental gradients, although some have examined competitive interactions in two different environmental settings (Erland & Finlay, 1992; Mamoun & Olivier, 1993; Mahmood, 2003; Lilleskov & Bruns, 2003; Koide *et al.*, 2005).

## III. Patterns of EMF competition

Bruns (1995) was the first to seriously discuss the role of competition in EMF communities. At the time that paper

was written, however, there was little empirical evidence that EMF species actually competed for root tips or soil resources. Most of the putative data came from field studies documenting changes in EMF composition on preinoculated seedlings, which was often interpreted to be the result of competition (e.g. Bledsoe *et al.*, 1982; Garbaye, 1983; McAfee & Fortin, 1986; Villeneuve *et al.*, 1991). Unfortunately, those studies all lacked an experimental design where the dynamics of the preinoculated EMF species were monitored in the absence of any competitors. Without that treatment it is impossible to know whether its performance was caused by the presence of other EMF species, the environmental conditions present, or an interaction between these factors. Since those early field studies, however, there have been a number of laboratory and field studies that have clearly documented competitive interactions among EMF species (Table 1). In fact, enough studies have accumulated that patterns have begun to emerge about the nature of EMF competition, which I summarize below and in Fig. 1.

### 1. Negative competitive effects are rarely reciprocal

When EMF species interact there are number of possible outcomes for the species involved (Tuininga, 2005). For pairwise interactions, outcomes are typically summarized with the symbols +, −, 0. Classic competition involves negative effects on both species, symbolized as −, −. Competitive effects can also be asymmetrical (*sensu* Connell, 1983 and should not be confused with asymmetric plant competition (Weiner, 1990)), with only one of the two species being negatively affected (−,0). If neither species is negatively affected, no measurable competition has occurred (0,0). (This classification scheme does not include a +/- interaction, which is typically used to designate parasitism or predation, as well as three-way or higher interactions, which involve both direct and indirect effects). In the EMF competition studies to date, there has been only one that clearly documented no negative competitive effects (Hortal *et al.*, 2008; *Rhizopogon luteolus* and *Lactarius deliciosus*). The general presence of negative competitive effects indicates that EMF competition is typically harmful to at least one of the interacting species. The effect on the other EMF species, however, appears to be variable and depends on whether root tips or soil are compared. Wu *et al.* (1999) examined competitive interactions among three EMF species and quantified the outcomes for both root tips and mycelia in real-time using clear plastic microcosms. In their pairing between *Suillus luteus* and *Pisolithus tinctorius*, competition did not affect each species' respective root tip colonization, but the mycelia of both species retracted after encountering each other, indicating a classic competitive interaction. Hortal *et al.* (2008) observed a different pattern between *L. deliciosus* and *Rhizopogon roseolus*, with a competitive effect of *Rhizopogon* on *Lactarius* decreasing root tip

colonization but not mycelial proliferation. In the second pairing of Wu *et al.* (1999), they observed an asymmetric interaction between an unidentified EMF species 'Tanashi 01' and *P. tinctorius*. Similarly, Kennedy & Bruns (2005), Kennedy *et al.* (2007a,b, 2009) have consistently observed only asymmetric interactions in root tip competition between species in the genus *Rhizopogon*. Interestingly, the mechanisms of these asymmetric interactions differed between studies. In Wu *et al.* (1999), the competitive effect of Tanashi 01 on *P. tinctorius* involved direct root tip and soil takeover (interference competition), whereas in those of Kennedy and colleagues, pre-emptive colonization (exploitation competition) by one *Rhizopogon* species suppressed the growth of its congeneric competitors. Although a larger number of studies are clearly needed, thus far it appears that in pairwise interactions competitive effects are rarely negative for both EMF species.

### 2. Competitive outcomes are environmentally context-dependent

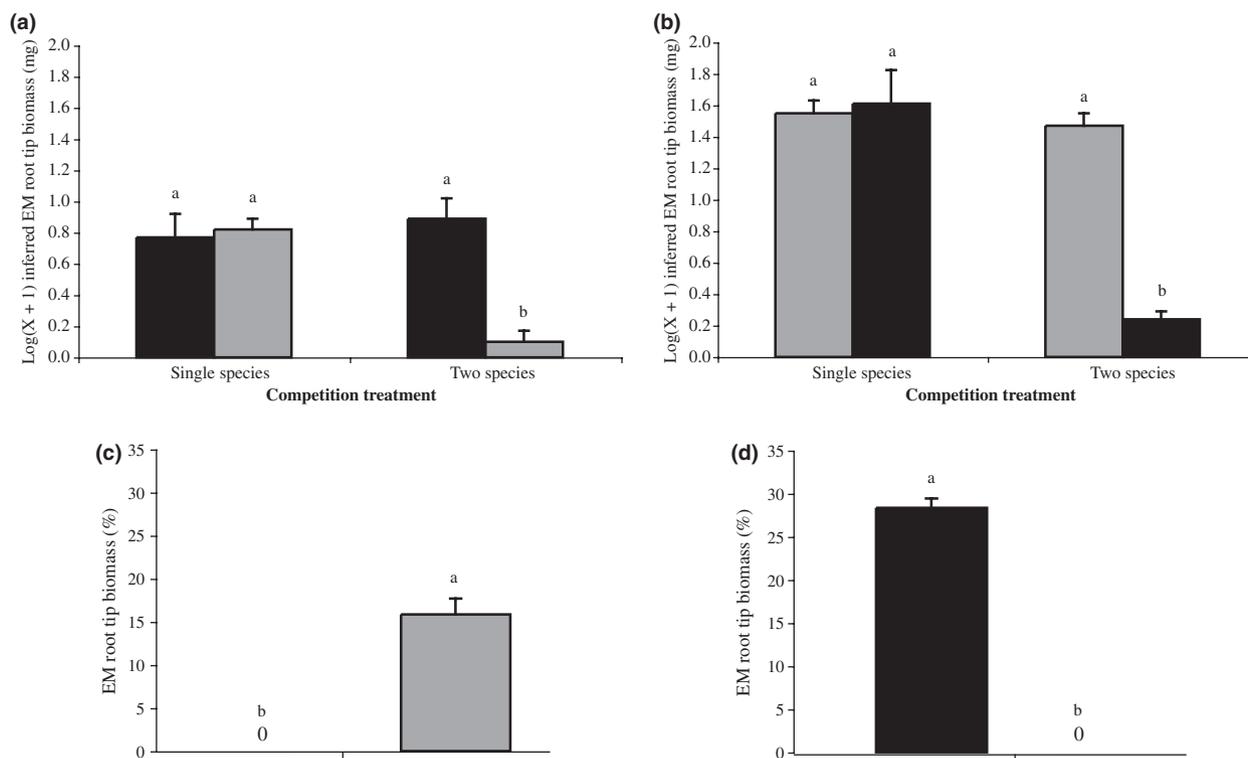
Many of the laboratory experiments of EMF competition have examined how environmental factors affect competitive outcomes. These studies can be grouped into those manipulating either abiotic or biotic factors. Erland & Finlay (1992) were the first to test an abiotic factor by examining temperature. In pairwise combinations of three EMF species maintained in 12°C and 20°C growth chambers, they found the outcome of competition varied with temperature, with weaker competitors at the lower temperature becoming competitive superiors or equivalents at the higher temperature. Another important abiotic factor for EMF species is soil pH (Erland & Taylor, 2002). Mahmood (2003) examined competition among two *Piloderma* species in a factorial experiment manipulating wood ash and nitrogen fertilizer. Addition of wood ash decreased the soil pH by 2 units and completely reversed the outcome of competition among the *Piloderma* species. While the ash also contained nutrients so the effect of pH was not isolated, the authors attributed the competitive reversal to the poor performance of *Piloderma croceum* at a nonoptimal pH (Erland *et al.*, 1990). In the same experiment, nitrogen addition also dramatically affected EMF competitive interactions. At low nitrogen concentrations, *P. croceum* was the dominant root tip competitor, but, at high nitrogen concentrations, *Piloderma* sp. 1 colonized significantly more root tips. Given that EMF competitive outcomes appear to be environmentally context-dependent and that abiotic factors vary considerably spatially and temporally in soil, a shifting mosaic of competitive dominance may help explain how the high richness of EMF communities is maintained.

In contrast to the aforementioned experiments, research on the effects of biotic factors on EMF competition attempt

**Table 1** Studies examining competition among ectomycorrhizal (EM) fungi

Competition	Study location	EM structure analysed	Assessment of competition	Type of analysis	Reference
Inferred	Field	Root tips	Change in species composition on root tips of precolonized seedlings	Morphotyping	Bledsoe <i>et al.</i> (1982); Garbaye (1983); McAfee & Fortin (1986); Villeneuve <i>et al.</i> (1991)
Inferred	Field	Root tips	Species co-occurrence patterns	RFLP, sequencing	Dahlberg <i>et al.</i> (1997)
Inferred	Field	Root tips	Physical mapping of species co-occurrences	Morphotyping	Agerer <i>et al.</i> (2002)
Inferred	Field	Root tips, mycelia	Species co-occurrence patterns with neutral models	tRFLP, sequencing	Koide <i>et al.</i> (2005)
Inferred	Field	Root tips	Species co-occurrence patterns with neutral models	Sequencing	Pickles <i>et al.</i> (2010)
Tested	Field	Root tips	Spore colonization of single and two-species inoculated EM seedlings	Real-time PCR	Kennedy <i>et al.</i> (2007a)
Tested	Field	Root tips, mycelia	Pre-colonized seedlings grown next to precolonized or NM seedlings	Real-time PCR, morphotyping	Hortal <i>et al.</i> (2008)
Inferred	Laboratory	Root tips	Precolonized seedlings inoculated with spores of a second species	Morphotyping	Mamoun & Olivier (1993)
Inferred	Laboratory	Root tips	Spore colonization of two-species inoculated EM seedlings	Morphotyping	Lilleskov & Bruns (2003)
Tested	Laboratory	Root tips	Precolonized EM seedlings added to microcosm with one NM seedling	RFLP, Morphotyping	Mahmood (2003)
Tested	Laboratory	Root tips, mycelia	Precolonized EM seedlings added to microcosm with many NM seedlings	Morphotyping, hyphal observation	Wu <i>et al.</i> (1999)
Tested	Laboratory	Mycelia	Precolonized seedlings grown next to precolonized seedlings	Real-time PCR, cloning, hyphal counts, DGGE	Landeweert <i>et al.</i> (2003)
Tested	Laboratory	Root tips, mycelia	Precolonized seedlings grown next to precolonized or NM seedlings	Real-time PCR, morphotyping	Parlade <i>et al.</i> (2007)
Tested	Laboratory	Root tips	Spore colonization of single and multispecies inoculated EM seedlings	RFLP, real-time PCR	Kennedy & Bruns (2005); Kennedy <i>et al.</i> (2007a, 2009)
Tested	Laboratory	Root tips	Hyphal and spore colonization of NM seedlings in replacement series design	Morphotyping	Parlade & Alvarez (1993)
Tested	Laboratory	Root tips	Precolonized seedlings grown next to precolonized seedlings	RFLP, isozyme	Timonen <i>et al.</i> (1997)
Tested	Laboratory	Root tips	Precolonized EM seedlings added to microcosm with one NM seedling	Morphotyping	Erland & Finlay (1992)

For competition, 'tested' refers to studies in which there was a comparison of single vs multiple species treatments; whereas 'inferred' refers to studies lacking single species treatments. EM, ectomycorrhizal; NM, nonectomycorrhizal; RFLP, restriction fragment length polymorphism; tRFLP, terminal restriction fragment length polymorphism.



**Fig. 1** Results of ectomycorrhizal (EM) fungal competition among *Rhizopogon salebrosus* (tinted columns) and *Rhizopogon occidentalis* (closed bars) in three different experiments. Within each sub-figure, different letters indicate significant differences among means (error bars represent +1 SE). (a) *Rhizopogon occidentalis* was competitively dominant in the field experiment of Kennedy *et al.* (2007a). (b) By contrast, *R. salebrosus* was competitively dominant in the laboratory experiment of Kennedy *et al.* (2007b). Reasons for the differences in outcomes are discussed in the latter experiment. In Kennedy *et al.* (2009), *Pinus muricata* seedlings were first inoculated from spores with one species, grown for 3 months, and then inoculated with an equal density of spores of a second species and grown for an additional 3 months. (c) Spores of *R. salebrosus* added first and then those of *R. occidentalis*. (d) Spores of *R. occidentalis* added first and then those of *R. salebrosus*. These results highlight three of the four major conclusions that can currently be drawn about EMF competition: negative effects are rarely reciprocal, outcomes depend on the environment in which they occur and timing of colonization matters.

to hold abiotic factors constant or, more precisely, do not systematically vary them across treatments. In these latter experiments, the factor manipulated is usually an aspect of the species being studied. Parlade & Alvarez (1993) examined competition among four EMF species, two host generalists (*Laccaria bicolor* and *Pisolithus arhizus*) and two host specialists (*R. roseolus* and *Rhizopogon subareolatus*). They found that the outcome of competition varied depending on the species pairing, with *L. bicolor* outcompeting both *Rhizopogon* species, but *P. arhizus* being competitively superior to *R. roseolus* and competitively inferior to *R. subareolatus*. These results suggest that host specificity is not a clear determinant of competitive ability; however, more tests of this question seem warranted (Palmer *et al.*, 2003). Timonen *et al.* (1997) simultaneously investigated both species and genotype competition by inoculating *Pinus sylvestris* seedlings with two genotypes of *Suillus bovinus* and a single genotype of *Suillus variegatus*. Although their experimental design was not completely factorial, they did find strong competitive interactions between both species and genotypes. In particular, the two genotypes of *S. bovinus* never colonized *P. sylvestris* roots at equal densities (one or the

other was always dominant), suggesting intraspecific EMF competition may be as strong as interspecific competition for some species. Kennedy *et al.* (2007b) conducted a third experiment on biotic effects by examining how the number of competitors affected the outcome of competition. Their experiment compared root tip competition among three *Rhizopogon* species in single-, two- and three-species treatment combinations. They found that in the two-species treatments *Rhizopogon vulgaris* and *Rhizopogon salebrosus* were competitive equivalents, but both outcompeted *Rhizopogon occidentalis*. However, in the three-species treatment, *R. vulgaris* colonized significantly more root tips than *R. salebrosus* and *R. occidentalis*. This result, like those described earlier, further indicates that competitive interactions are abiotically and biotically environmentally context-dependent.

### 3. Field distributions often reflect competitive interactions

Laboratory studies have clearly documented that EMF species compete for host root tips and space in soil, but

studies done in the field and at the community level are needed to confirm the ecological relevance of these findings. Field community studies have two advantages over laboratory experiments because they examine: nonculturable EMF species, which represent the majority of EMF species; and entire EMF communities rather than simplified two or three-species groupings. However, as mentioned previously, manipulating EMF communities in ways that conform to experimental designs needed to assess competitive interactions is more challenging than similar experiments on other organisms. Therefore a number of EMF studies have relied on naturally occurring species distribution patterns to infer the existence of competitive interactions. The most commonly used technique is to document 'checkerboard' distributions (*sensu* Diamond, 1975), where certain species combinations are never or very rarely found together in the same location. The lack of overlap in distribution is assumed to be caused by competition, as two equivalent species cannot occupy the same location at the same time (i.e. competitive exclusion principle). While 'checkerboard' distributions are often the result of competition, it is important to note that other ecological and evolutionary factors can generate similar co-occurrence patterns (Gotelli & McCabe, 2002), so additional experiments should be conducted to confirm that competition is actually the primary determinant of the observed species distributions.

With that caveat in mind, studies from a wide range of systems have found EMF field distributions consistent with the presence of competitive interactions. Examining the EMF community in a *Picea* forest, Dahlberg *et al.* (1997) reported a 'checkerboard' distribution between two of their most abundant species, *P. croceum* and *Tylospora fibrillosa*. They observed a complete lack of co-occurrence of root tips of the two species in 2.25 cm<sup>2</sup> soil cores, suggesting strong competitive interactions at the cm<sup>2</sup> scale. Agerer *et al.* (2002) used a 'micromapping' approach to look at EMF species co-occurrence in 25 cm<sup>2</sup> field soil grids. They also found patterns of significant negative as well as positive species co-occurrence. The most robust test of 'checkerboard' distributions was conducted by Koide *et al.* (2005), who looked at patterns of EMF species root tip co-occurrence in soil cores taken in a *Pinus resinosa* stand over a 13-month period. Along with greater spatial and temporal replication, this test was more robust than previous co-occurrence studies because the authors used a statistical method to generate a null distribution model against which their observed species distributions could be compared (Stone & Roberts, 1990). They found that co-occurrence was significantly lower than expected by random chance, particularly among the most abundant EMF species, which strongly suggested that competitive interactions were a primary determinant of EMF community structure in that stand. Most recently, Pickles *et al.* (2010) examined community co-occurrence patterns over a 2-yr period in a *Pinus sylvestris* plantation.

They too found considerable evidence of both negative and positive species co-occurrences, although some species pairings changed in direction between years, apparently owing to differing environmental conditions. Collectively, these studies suggest that competition can have a significant effect on EMF species field distributions and may also play an important role in structuring EMF communities.

#### 4. Timing of colonization influences competitive success

Ectomycorrhizal fungus species may use many strategies to gain an advantage over their competitors. Some of the possible mechanisms include direct interactions such as sporophagy (Fries & Swedjemark, 1985), mycoparasitism (Agerer, 1990), mycelial overgrowth (Wu *et al.*, 1999) or indirect interactions mediated through the plant (see below). Another way that EMF species can gain a competitive advantage is by colonizing resources ahead of their competitors. This type of advantage is typically referred to as a 'priority effect' because the early colonists negatively affect the later arrivers through preemption of a shared resource. Kennedy & Bruns (2005) documented a strong priority effect between two EMF species, *R. occidentalis* and *R. salebrosus*, colonizing *Pinus muricata* seedlings from spores. They found that the more rapid spore germination and root tip colonization of *R. occidentalis* resulted in the almost complete exclusion of *R. salebrosus* from their two-species treatment. This laboratory result was later confirmed in a similarly designed field experiment conducted over a longer period (Kennedy *et al.*, 2007a). While both of those studies suggested a priority effect was occurring, a more rigorous test would involve experimentally reversing the order of species colonization to see if competitive outcomes changed. Kennedy *et al.* (2009) set up that type of experiment with four *Rhizopogon* species in which seedlings were first inoculated with spores from one species, grown for 3 months, and then inoculated with an equal density of spores of second species and grown for an additional 3 months in all pairwise combinations. For three of four species investigated, the timing of colonization completely determined competitive success. For example, when *R. salebrosus* was inoculated onto seedlings before *R. occidentalis*, it excluded the latter species from colonizing any root tips, which in combination with the results from the previous studies, clearly indicate that timing, rather than other factors, can determine EMF competitive outcomes. It appears, however, the strength of priority effects depends on the proportion of root tips colonized as Kennedy *et al.* (2009) found that relatively low initial colonization by *R. evadens* did not inhibit subsequent colonization by two of the other three *Rhizopogon* species.

Although multiple studies have documented priority effects among EMF species, others have shown that that

timing of colonization is not always a primary determinant of competitive success. This was most clearly demonstrated by Wu *et al.* (1999), who observed root tips and soil first colonized by *P. tinctorius* later directly taken over the unidentified EMF species 'Tanashi 01'. A similar pattern was observed by Lilleskov & Bruns (2003), who found that *R. occidentalis* initially colonized most of the root tips in their *P. muricata* microcosms, but *Tomentella sublilacina* became the dominant root tip colonizer over time. In the latter study, however, the researchers did not include single-species treatments in their experimental design, so it is not clear if the decline of *R. occidentalis* was caused by *T. sublilacina* or some other factor. The importance of single-species treatments in EMF competition studies was particularly well illustrated by Landeweert *et al.* (2003). Those researchers examined the interactions between *S. bovinus* and *Paxillus involutus* and found a complete reversal in the abundance of each species in their two-species treatment over time. While this result suggested that priority effects were not important, the performance of each species in the single-species treatments were very similar to the two-species treatment, indicating that the change in mycelial abundance was unrelated to competition. The relative importance of priority effects may also be influenced by the relatedness of fungal competitors. Owing to greater functional similarity, priority effects may be stronger among closely related species, particularly if plants differentially reward functionally different EMF species. As such, future studies examining a wider range of EMF species will help in determining the general role that priority effects play in EMF competition.

Before moving on, it is also important to consider the effect of temporal scale on the aforementioned conclusions. Factors such as the speed at which spores germinate and the rate of spread of mycelium are most significant at shorter temporal scales (weeks to months), particularly in competitive interactions where priority effects are important. However, it appears that many EMF competitive outcomes are not necessarily permanent. For example, Lian *et al.* (2006) documented significant declines in EMF species richness within the active band of *Tricholoma matsutake* 'fairy rings', however, both inside and outside of the rings EMF richness was much higher. The recovery inside the fairy rings suggests that while competitive effects can strongly alter community composition at a single time-point, when a dominant species is no longer present, competitively inferior species can quickly recolonize. The interaction between time and competition is also apparent when considering different life-history stages of EMF species. For example, the competitive dominance of *R. occidentalis* over *R. salebrosus* in both laboratory (Kennedy & Bruns, 2005) and field experiments (Kennedy *et al.*, 2007a) does not correspond with their natural distributions. Both species are present in young *P. muricata* forests (Peay *et al.*, 2007), but only *R. salebrosus* is present in older *P. muricata*

forests (Gardes & Bruns, 1996). So how does this putatively weaker competitor (*R. salebrosus*) persist? The initial competitive outcome between these two species is driven completely by timing of spore germination, as described earlier. However, it appears that while *R. salebrosus* has slower-germinating spores, once competition has shifted from spore- to mycelial-based interactions, *R. salebrosus* is actually the stronger competitor (Kennedy *et al.*, 2007a; P Kennedy, unpublished). This pattern is consistent with many of the longer term (years to decades) successional shifts observed in EMF communities (Deacon & Fleming, 1992) and may explain why certain EMF species are competitive dominants at one time and competitive inferiors at another (e.g. Lilleskov & Bruns, 2003). A final temporal factor affecting EMF competition involves the life-span of host roots. While there is still debate about actual life-span of fine roots (somewhere between months and years) (Gaul *et al.*, 2009), Hoeksema & Kummel (2003) used a simple ecological model to demonstrate that changes in root life-span could dramatically alter EMF competitive dynamics, particularly if plants can selectively control life-span based on symbiont effectiveness. Although it would certainly be more convenient for EMF researchers if competitive outcomes had greater temporal predictability, I hope the observed variation will not deter further research but rather embolden it.

#### IV. How do EMF competitors coexist?

On the surface, the presence of strong competitive interactions among EMF species is paradoxical with the typically high diversity of EMF communities (*sensu* Hutchinson, 1961). One would predict that mature EMF communities should only be occupied by a handful of competitive dominants, yet most contain a long 'tail' of rarer species that have not been competitively excluded. Thus, a part of the maintenance of high EMF community diversity must involve mechanisms that promote competitive coexistence. Bruns (1995) highlighted four ways that EMF competitors could coexist in a small and homogeneous host environment: niche partitioning, disturbance-related patch dynamics, density-dependent mortality and competitive networks. Next I will discuss three additional mechanisms for which there is recent data related to EMF species. It is important to note that these mechanisms should not be considered mutually exclusive. For example, in the *P. muricata* forests studied by Bruns and colleagues, niche partitioning (Taylor & Bruns, 1999), disturbance (Horton *et al.*, 1998; Baar *et al.*, 1999), competition-colonization tradeoffs (Peay *et al.*, 2007), storage and priority effects (Bruns *et al.*, 2009; Kennedy *et al.*, 2009) all appear to contribute to species coexistence. In addition, some mechanisms of coexistence require environmental fluctuations (but not necessarily disturbance *per se*) to work, while others can occur in environments that are homogeneous (Chesson,

2000). The first two mechanisms I discuss, lottery models and storage effects, both require environmental heterogeneity. By contrast, competition–colonization trade-offs, can promote coexistence in homogeneous environments.

The first coexistence mechanism has been referred to as the lottery hypothesis because ‘the species of a guild are competing in a lottery for living space in which larvae are tickets and the first arrival at a vacant site wins that site’ (Sale, 1977). This mechanism has a number of assumptions: that space is a limiting resource, that vacant space is recolonized by the first-available recruit, that there are strong priority effects in space occupancy (i.e. original colonists are not displaced through competitive hierarchies), and that environmental fluctuations cause individual species recruitment to vary spatially and temporally (Chesson & Warner, 1981). While there is limited information about many of these assumptions for most EMF species, the EMF community present in young *P. muricata* forests seems to have many lottery-like features. In particular, a suite of *Rhizopogon* species (specifically *R. occidentalis*, *R. salebrosus* and *R. vulgaris*) have very similar life-histories and their coexistence is not well explained by differing competitive abilities. The spores of these species are widely codispersed by animals and they are among the dominant colonizers of young *P. muricata* individuals (Horton *et al.*, 1998; Baar *et al.*, 1999; Peay *et al.*, 2007). In those forests, space does appear to be a limited resource because nearly all fine roots are colonized by EMF species (P Kennedy, pers. obs.). Non-mycorrhizal roots of young *P. muricata* individuals are rapidly colonized by *Rhizopogon* species, particularly in primary successional settings, (Horton *et al.*, 1998) and specific species composition varies depending on local spore density (P Kennedy & T Bruns, unpublished; see Izzo *et al.* (2006) for analogous data in another California conifer forest). As noted previously, the outcome of competitive interactions among these *Rhizopogon* species is clearly driven by priority effects (Kennedy *et al.*, 2009) and community dominance by this group has been maintained over the first 12 yr of forest succession (Baar *et al.*, 1999; Peay *et al.*, 2007). Taken together, this data suggests that a ‘lottery’ for root space driven by widespread spore dispersal, rapid colonization, and strong priority effects appear to be a good explanation of the coexistence among these EMF competitors.

A second way that EMF competitors may coexist involves differential recruitment over time. If fluctuating environmental conditions favor the recruitment of different EMF species in different years, this would allow competitors to be present in the same EMF community. This type of species coexistence has been referred to as ‘the storage effect’ because adult populations buffer the influence of environmental fluctuations on recruitment (Warner & Chesson, 1985). One way adults can buffer environmental fluctuations is by producing propagules that are capable of surviving long periods of unfavorable recruitment conditions.

Little is known about storage effects for most EMF species, but many species in genus *Rhizopogon*, including those just mentioned, appear to coexist in EMF communities by producing spores that persist in soils for very long periods of time. Bruns *et al.* (2009) elegantly documented no decline over a 4-yr period in the colonization of *P. muricata* seedlings annually planted into the same *Rhizopogon* spore-inoculated soils. Those researchers found that less spores were needed to get equivalent levels of colonization as their experiment progressed, indicating that spore longevity among certain *Rhizopogon* species is likely in the order of decades. This longevity seems to be essential for persistence because while *Rhizopogon* species make up a dominant part of the EMF communities in young *P. muricata* forests (Baar *et al.*, 1999; Peay *et al.*, 2007), they are largely absent from mature *P. muricata* forests (Gardes & Bruns, 1996). The presence of periodic stand-replacing fires creates the opportunity for *Rhizopogon* species to recolonize their host, replenish their ‘spore bank’, and then wait until favorable conditions for their recruitment appear again.

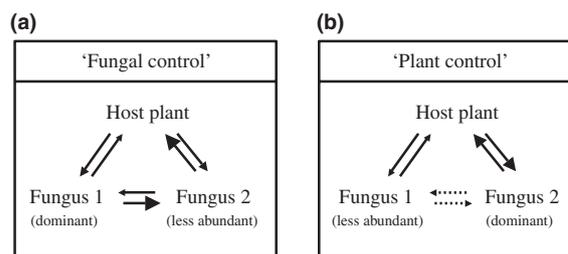
A third way that EMF species can coexist relates to trade-offs in species’ life-histories. It has been shown, for example, that plants vary in their ability to disperse vs compete and that this trade-off is responsible for maintaining the high species richness present in certain grassland communities (Tilman, 1994). For EMF species, a colonization–competition trade-off would involve allocating resources to either vegetative structures such as extraradical mycelia, which are essential for colonizing new root tips and competing for soil nutrients and water, or to fruiting bodies and their associated spores. This relationship was examined by Peay *et al.* (2007) in a unique experimental system, where a major fire created a series of *P. muricata* ‘tree islands’ that differed in both size and distance from the unburned forest. They found that species that occurred widely and colonized small islands tended to be those that invested the most in dispersal structure relative to vegetative structures. For example, *Suillus pungens*, which occurred on every island surveyed, was found in 43% of fruit body samples but only 13% of root tip samples, while *Russula amoenolens*, which was found only on the largest islands, was present in only 23% of fruit body samples but in 35% of root tip samples. While direct studies of dispersal rates and competitive interactions across a wider range of EMF species are needed to more robustly determine the existence of this putative trade-off, the data from Peay *et al.* (2007) indicate that differences in colonization and competitive abilities may facilitate species co-existence in EMF communities.

As noted by Bruns (1995) and others (Palmer *et al.*, 2003), it is unlikely that any single mechanism will be able to fully explain how competitors coexist in a given community. As such, it seems more productive for EMF ecologists to focus on the relative contributions of different mechanisms rather than to search for a single ‘holy-grail’

explanation of coexistence. Conducting similarly-designed experiments in different systems (*sensu* Callaway *et al.*, 2002) will greatly facilitate our understanding of the global significance of different mechanisms. Another factor regarding explanations of EMF coexistence is the explicit consideration of spatial and temporal scale. For example, analyses focused at local spatial scales (e.g. within soil cores) are likely to find that interactions such as competition have a large effect on coexistence, while analyses done at landscape spatial scales will likely indicate that host plant composition and dispersal are more important determinants. Similarly, certain factors such as the timing/quantity of carbon allocation are likely more significant at shorter time-scales, whereas factors like host plant composition are more important at longer time-scales. Although this kind of scale-dependent perspective is intuitive, common in ecology and has been crucial in clarifying debates about different mechanisms of coexistence (Bengtsson *et al.*, 1994; Chesson, 2000), EMF ecologists have only recently become to think in these terms (Bruns & Kennedy, 2009).

## V. Unanswered questions and future directions

Despite the considerable number of studies done on EMF competition, there are still many unanswered questions. We still know very little, for example, about how exactly EMF species compete for roots or nutrients in soil. Are they producing antifungal compounds that can be used to hold territory or take over poorly defended resources? There has been good documentation of these kinds of chemical interactions in non-EMF fungal competition (Shearer, 1995) and certain EMF species have been shown to produce antifungal compounds (Krywolap, 1964; Duchesne *et al.*, 1988). The generality of these findings, however, is currently unknown and studies of gene expression or metabolite production in single species and multispecies settings would greatly assist in determining specific competitive mechanisms. Another major unanswered question is exactly how EMF species and their hosts interact. Plants are typically simultaneously colonized by many EMF species, but it is unclear which partner in this symbiosis controls which EMF species are present (Fig. 2). One possibility is that the fungi themselves compete directly for root tip colonization and the plant is a passive participant in this process (Fig. 2a). Assuming mutualisms are based on reciprocal exploitation, one would predict that superior competitors may use resources normally traded to their host to outcompete other EMF species for new root tips (e.g. greater investment in nitrogen- or phosphorus-rich antagonistic compounds). This would imply that the best EMF competitors are also the poorest symbionts, which could lead to a breakdown in the symbiosis over time (Sachs & Simms, 2006). Alternatively, plants may be the primary determinant of EMF composition on their roots (Fig. 2b; Kummel &



**Fig. 2** Two different scenarios of partner control in the ecto-mycorrhizal fungal (EMF) symbiosis. Arrow size corresponds to a given amount of resources being used/traded. In scenario (a) EMF species would use resources typically traded to the host plant for antagonistic interactions against other EMF species. This type of direct interference competition could occur through the production of nitrogen or phosphorus rich antifungal compounds, which would allow more antagonistic species to dominate host plant root space. This scenario assumes that the plant cannot sanction less beneficial EMF species, although there is recent evidence to the contrary (Nehls *et al.*, 2007). In scenario (b), the plant preferentially allocates carbon to the EMF species that provides it with the most resources. Because the amount of carbon provided is proportional to the resources received, this would discourage investment in antagonistic compounds (the dotting on the fungal interaction arrows is to indicate this interaction would be negligible in this scenario). To examine which of these two scenarios is more likely, host plants colonized with two different EMF species (ideally ones providing different quantities of the same resource) could be grown in two types of split-root microcosms. The first type of microcosm would have the two species physically isolated from each other, so their only interaction would be through the shared host. The second type would allow the two species also interact directly as through their shared host (e.g. without the split-root barrier). If species 1 had higher colonization when direct interactions were possible but not when physically isolated, this would suggest fungal control is a stronger determinant of EMF colonization. Alternatively, if species 2 had higher colonization when direct interactions were possible and when physically isolated, this would suggest host plants have primary control over EMF colonization.

Salant, 2006). If this is the case, it would mean that EMF species more likely compete with each other indirectly (i.e. through the plant) for host carbon. The species that give more to the host and do not invest in antagonistic compounds would likely be rewarded disproportionately, making the best EMF competitors also the best symbionts and favoring stability in the EMF symbiosis. These two scenarios represent opposite ends of a continuum; where plants and EMF species fall along it is still very much open to debate. A third related question about EMF competitive dynamics is how these fungi interact with different hosts. It appears that most EMF species have the ability to colonize multiple co-occurring hosts (Molina *et al.*, 1992), although many show preferences for certain hosts over others (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008; Smith *et al.*, 2009). Assuming that the quantity of carbon provided to EMF species is not identical across host taxa (a major untested assumption), a species may be strong mycelial competitor on one host, but a weak one on another (see below for a putative test of this question in AMF communities). Similarly, on any given

host, if certain EMF species can extract more carbon per root tip than other species (Bidartondo *et al.*, 2001), it is likely to have a competitive advantage. Studies from the ecological literature have also shown that interspecific competition can be mediated by interactions with other trophic levels. For example, preferential consumption of a competitive superior by a generalist predator can allow competitively inferior species to persist in the same habitat (Paine, 1974). This type of interaction has been elegantly demonstrated among saprotrophic fungi (Parkinson *et al.*, 1979; Newell, 1984), but how fungal grazers influence the outcome of EMF competition remains untested. While these questions are by no means an exhaustive list, their answers would provide considerable insight how EMF species compete as well as the nature of the EMF symbiosis itself.

In addition to the aforementioned questions, future studies of EMF competition will also benefit from the inclusion of a broader range of species. Thus far there has been a strong bias in experimental studies towards species in the genus *Rhizopogon*. Much of this bias reflects the relative ease of manipulating species in this genus to create the single-species and multispecies treatments needed to assess competition. However, this genus is not dominant or even present in most EMF forests and new studies with species from different genera are needed to expand the ecological breadth and realism of EMF competition research. Specifically, comparing a wider range of EMF genera will allow researchers to better link different functional traits (e.g. hyphal foraging types, utilization of organic nitrogen or phosphorus sources, drought tolerance) with competitive success, which will help in determining how EMF species compete. Although culturing representatives from other genera (e.g. *Russula*, *Cortinarius*, *Inocybe*, *Tomentella*, *Thelephora*) for new competition experiments is likely to be challenging, studies such as that of Nara (2006) indicate it is possible to do community-level experiments with species from many EMF genera. Another trend in the EMF competition literature has been the ubiquitous use of conifer host plants, particularly members of the Pinaceae. While conifer hosts are ecologically and economically important, there are many other angiosperm EMF hosts, particularly in the southern hemisphere, for which EMF competitive interactions have yet to be examined. If hosts vary in their trading relationships with EMF species, these differences could have significant effects on EMF competition, particularly in mixed-species forests where the same EMF species may be present on multiple hosts. A third area that will provide important new information are studies examining environmental gradients. Studies of plant competition indicate that competition intensity varies greatly depending on nutrient conditions (Grace & Tilman, 1990; Sammul *et al.*, 2006), but similar effects on EMF competition are not well understood. Koide *et al.* (2005) observed a decrease in EMF competitive interactions in nitrogen-amended plots,

suggesting that in higher nutrient sites, EMF competition may be less intense. These results, however, reflect a single study comparing a single nutrient at a single level of addition. True gradient studies need to incorporate at least three (and ideally more) treatments to determine the shape of EMF competition response curves as the factor of interest changes. Nutrient and water gradients are obvious choices for future studies, but examining EMF competition intensity along other gradients, for example different aged forests or different carbon dioxide concentrations, would also provide further insight into how EMF communities change over space and time.

## VI. New methods and approaches

New methodologies and more complex experimental designs hold much promise for more fully understanding EMF competitive dynamics. Isotopic methods are likely to be particularly helpful because they address function-related questions and can simultaneously investigate both sides of the symbiosis (Leake *et al.*, 2004; Hobbie, 2005). A limitation of these methods to study of competition, however, is that in multispecies settings determining which individual EMF species are receiving or transferring resources is challenging because only bulk flows are examined. Thus, adopting isotopic methods for competition studies will require experimental designs where EMF species interacting with the same host plant are physically isolated. This can be accomplished with split-root experiments (Lilleskov & Bruns, 2003; Kennedy *et al.*, 2009; Bever *et al.*, 2009), which have been largely underexploited by EMF ecologists. Stable isotope probing is a newer method that combines isotopic analysis with molecular identification, therefore allowing for species-specific functional analyses in multispecies settings (Radajewski *et al.*, 2003). Although this method has been widely adopted to analyse the function of unculturable prokaryotes (Dumont & Murrell, 2005), it is has yet to permeate EMF ecology. Vandenkoornhuys *et al.* (2007) successfully used stable isotope probing to analyse the activity of AMF communities associated with three plant species and found that while many species were present on multiple hosts, their activity (as defined by  $^{13}\text{C}$ -labeled rRNA) varied considerably across hosts. They speculated that the observed variation was a consequence of within-root AMF competition on different hosts. Combining this newer isotopic technique with more innovative experimental designs (e.g. comparing split-root chambers where the barrier between individual chambers is removed or left intact) would allow for significant inferences to be drawn about how EMF function is connected with competitive success.

Another method that has been increasingly used to study EMF competition is real-time PCR. Unlike end-point PCR, this method uses specific primers and/or probes in combination with fluorescence chemistry to quantify the

amount of target material present in a sample (Smith & Osborn, 2009). Like stable isotope probing, the ability to independently quantify individual species' abundances in multispecies settings is well suited for EMF competition experiments. This method has the additional advantage over endpoint PCR of greater sensitivity to detect extremely small quantities of DNA template (Smith & Osborn, 2009). Real-time PCR was first used to examine EMF competitive interactions by Landeweert *et al.* (2003) described earlier. It was used similarly by Parlade *et al.* (2007) and Hortal *et al.* (2008) to investigate hyphal competition among *L. deliciosus* and *Rhizopogon* species. While most of the EMF studies using real-time PCR have focused on quantifying mycelium (including noncompetition studies: Schubert *et al.*, 2003; Raidl *et al.*, 2005; Wolfe *et al.*, 2010), Kennedy *et al.* (2007a,b) have also successfully used this method to examine root tip competition among *Rhizopogon* species. Importantly, the results generated from real-time PCR have generally corresponded with those produced by other methods. For example, Landeweert *et al.* (2003) simultaneously tested two other molecular quantification methods (denaturing gradient gel electrophoresis and cloning) and the results of all three methods were qualitatively similar. Similarly, the real-time PCR results of Kennedy *et al.* (2007a) matched closely with those of a similarly designed experiment that used endpoint PCR to quantify EMF root tip competition (Kennedy & Bruns, 2005).

Although the quantitative aspect and higher sensitivity of real-time PCR are attractive for studies of EMF competition, a number of precautions must be taken to insure that results have accurate biological meaning. One of the primary concerns for EMF competition studies is the use of the internal transcribed spacer (ITS) region for quantification. As the number of ITS copies can vary considerably among EMF species (Debaud *et al.*, 1999), similar amounts of fungal ITS rDNA do not necessarily correlate with similar amounts of fungal biomass (Landeweert *et al.*, 2003). Unless there are attempts at correcting for species-specific differences (Kennedy *et al.*, 2007a,b) or careful correlations between hyphal length/biomass and ITS copy number (Raidl *et al.*, 2005), comparisons of ITS-based real-time PCR data among EMF species must be interpreted with caution (Landeweert *et al.*, 2003). In addition, calculated quantities of EMF mycelium or root tips in real-time PCR analyses are entirely dependent on the standard used. Parlade *et al.* (2007) found that mycelial standards of *L. deliciosus* with identical weights had very different  $C_t$  values (the level at which template fluorescence exceeds background fluorescence) depending on the age of the culture used. Therefore, care must be taken that standards of all the species used in competition experiments are of equivalent ages to ensure that interspecific differences are correctly compared. Age variation in samples themselves may also

lead to difficulties in applying this method. For example, Kennedy *et al.* (2007b) was unable to include a fourth *Rhizopogon* species in their analyses because of a poor correlation between actual root tip weights and those inferred from real-time PCR, which was most likely caused by greater age variation in the tips of that species. Given these challenges and others (Smith & Osborn, 2009), additional optimization efforts will greatly benefit the use of this method in future EMF competition studies.

A third method gaining popularity among ecologists is the incorporation of phylogenetic data into community ecology studies (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). These analyses are based on the idea that if important functional traits have strong evolutionary patterns then the distribution of organisms in the environment will not be random with respect to phylogeny. For example, when competitive exclusion is important and phenotypic traits are evolutionarily conserved (e.g. closely related species use the same resources), then closely related species should be less likely to co-occur (Webb *et al.*, 2002). Alternatively, when tolerating particular environmental conditions is important (environmental filtering) then conserved phenotypic traits would result in closely related species colonizing the same habitat more successfully than distantly related species (e.g. colonization of a habitat with only organic nitrogen present, which only certain EMF groups can metabolize; Abuzinadah & Read, 1986). Peay *et al.* (2010) recently used these methods to examine the phylogenetic structuring of EMF communities present across a soil ecotone in a lowland rainforest in Borneo. They found evidence that EM species within a soil habitat tended to be more closely related and suggested that this was because of conservation of functional traits within particular lineages. The use of phylogenetic community analyses, however, requires careful consideration of alternative hypotheses (Kraft *et al.*, 2007). Different processes can generate the same nonrandom pattern depending on whether traits are conserved or convergent, so direct experimentation is necessary to determine exactly which processes are occurring. For example, the absence of a phylogenetic pattern consistent with competition does not mean that this process is not occurring, but rather that closely related species are not competing more strongly than distantly related species. The scale of sampling can also dramatically affect the conclusions drawn (e.g. competition may be important at small scales and habitat filtering important at larger scales), so studies examining phylogenetic community patterns need to test them at multiple spatial scales (Webb *et al.*, 2002; Kraft & Ackerly, 2010). Despite these issues, a major advantage of these methods, particularly of beta-diversity analyses, is that plots or studies that do not share any species can be compared statistically, which may allow for global generalizations about the factors determining EMF community assembly and diversity (Dickie & Moyersoen, 2008).

## VII. Conclusions

The future of studying EMF competition looks bright for a number of reasons. The first is the growing interaction between fungal and general ecologists (Kennedy & Bruns, 2007). Much of the ecological theory about competition and coexistence has been developed from studies of larger organisms and fungi represent a unique hybrid of macroscopic and microscopic worlds (Peay *et al.*, 2008). As such, they may provide an important bridge in searching for ecological generalities across the major domains of life (Prosser *et al.*, 2007). Second, the widespread adoption of molecular identification and quantification techniques has taken away many of the barriers that existed for studying EMF communities (Horton & Bruns, 2001). While the use of these techniques requires knowledge about their limitations, researchers are consistently using molecular methods to ask sophisticated questions about EMF competition. Third, the increasingly interdisciplinary approach of EMF ecologists (e.g. microscopic, isotopic, phylogenetic and statistical methods), combined with greater laboratory and field experimentation, has shifted the focus of EMF community studies from pattern to process and to seek a global perspective. Finally, in an era of unprecedented anthropogenic change, better understanding how different factors such as competition affect EMF community structure will be essential for preserving and restoring this ecologically essential symbiosis.

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