Chapter 1
Mycorrhiza Specificity: Its Role in the Development and Function of Common Mycelial Networks

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Abstract The establishment of common mycelial networks by mycorrhizal fungi shared between host plants depends on the ability of neighboring plants to enter into mycorrhizal associations with compatible fungal species. Such compatibility is governed by the potential mycorrhiza specificities of the symbionts. Mycorrhiza specificities exist along a continuum from low specificity (association with multiple partners) to high specificity (association with one or few partners). Although the ability of symbionts to form mycorrhizas may be largely governed by host-fungus gene interactions as influenced by co-evolutionary events, mycorrhizal associations in natural ecosystems can also be influenced by environmental factors (e.g. soil) and biological factors (e.g. different neighboring host species), phenomena referred to as "ecological specificity." For example, in natural settings, mycorrhizal fungi often express "host preference" wherein fungi may be more common on a particular host in mixed-host settings than would be expected by random species assemblage within the fungal and plant communities. Mycorrhiza specificity phenomena significantly influence plant community dynamics, particularly plant succession. Early seral plants can positively affect the establishment of later-seral plants by maintaining commonly shared mycorrhizal fungi, and thus affecting the function of common mycelial networks over time. Such knowledge provides guidance for ecosystem managers to maintain "legacy" early -seral plants that benefit later-seral plants via shared mycorrhizal fungus species. Understanding specificity phenomena is also crucial for predicting the successful migration of plants and compatible mycorrhizal fungi during climate change. We review mycorrhiza specificity terminology and types of specificity phenomena, and suggest use of common terms to

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provide consistency in addressing this research topic. We also provide extensive examples from diverse ecosystems on the ability (or inability) of neighboring plants to develop common mycelial networks.

Keywords Host specificity · Mycorrhiza specificity · Mycorrhiza compatibility · Host preference · Ectomycorrhiza

1.1 Introduction

Common mycelial networks (CMNs) of mycorrhizal fungi connecting neighboring host plants affect ecosystem processes and community dynamics including seedling establishment, plant succession, and ecosystem resiliency (Simard et al. 2002, 2012; Simard and Durall 2004; Simard and Austin 2010; Selosse et al. 2006; Horton and van der Heijden 2008; van der Heijden and Horton 2009). Requisite to the establishment and function of CMNs is the ability of neighboring plants to be colonized by shared mycorrhizal fungi, or more specifically, individuals with continuous mycelial systems. Formation of linkages via compatible mycorrhizal fungi is governed in large part by the potential mycorrhiza specificities of the symbionts (i.e., host range of fungus, fungus range of host).

Molina et al. (1992) comprehensively synthesized concepts, phenomena, and ecological implications of mycorrhiza specificity. In the ensuing 20 years, many researchers have expanded upon those ideas to support an overarching concept: the degree of specificity displayed by both plant and fungal symbionts varies along a continuum from low specificity (associate with many symbiotic species) to high specificity (associate with one or a few species) (Fig. 1.1).

Several general terms are used to express where the symbionts lie along this continuum. For example, fungi only known to associate with a particular host species, or, more commonly, a host genus or family, are called "host specialists" for that host taxon. Those fungi that show less or no restriction to a taxonomic group of hosts are commonly called "generalists". Taylor et al. (2002) note that the "degree of specificity is a unique attribute of each partner". Although we can use general terms to describe similarities among fungi and hosts in mycorrhiza specificity

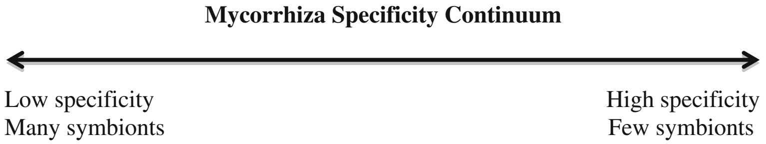

Fig. 1.1 Specificity continuum. Symbiotic plants and fungi fall along a continuum of specificity patterns. These interactions influence the complexity (number and diversity of species) of a mycorrhizal network

attributes, we must recognize that such general terms are relative and require more precise definition within the context of a study or when comparing studies. One of our goals is to bring clarity in the use of terms relevant to describing mycorrhiza specificity phenomena.

Mycorrhiza specificity processes and phenomena are complex due to the high diversity of mycorrhizal symbionts that span a phylogenetically diverse group of plant and fungal taxa, forming a variety of mycorrhizal types (e.g., arbuscular-, ecto-, orchid-, and ericoid mycorrhiza) with varied evolutionary histories (Hibbett and Matheny 2009; Tedersoo et al. 2010a; van der Heijden et al. 2015). Such complexity challenges our ability to generalize about global patterns of mycorrhiza specificity because we continually discover exceptions as we explore new ecosystems. A commonly cited generalization from the Molina et al. (1992) review, for example, is that most mycorrhizal fungi display a broad host range (or that little specificity is expressed in mycorrhizal associations). While this generalization may be true in a numerical sense, those same authors also provided numerous examples of fungi that showed variously restricted levels of host specificity and cautioned about over generalizing about these patterns. Since that 1992 review several papers support both the widespread nature of generalists and specialists among ectomycorrhizal (EM) fungi, and shed light on how host community composition and ecological conditions at a site impacts the relative abundance and function of EM fungi along the specificity continuum.

Concepts of mycorrhiza specificity go beyond a simple understanding of whether particular plants and fungi can enter into a mycorrhizal symbiosis. Harley and Smith (1983) coined the term “ecological specificity” to emphasize that the ability of plants and fungi to form mycorrhizae in the field may differ from that demonstrated in experimental syntheses wherein the symbionts are brought into contact under controlled conditions. Ecological specificity may be thought of as a variation on the ecological concepts of fundamental and realized niches. Molina et al. (1992) expanded this concept to include how a diversity of abiotic and biotic factors may affect the ability of plants and fungi to develop mycorrhizae in nature. This is analogous to applying the disease triangle in plant pathology (Fig. 1.2). The presence and composition of neighboring plants can affect the ability of some mycorrhizal fungi to develop mycorrhizae with particular hosts (Massicotte et al. 1994; Molina et al. 1997; Simard et al. 1997a; Kohout et al. 2011). As will be discussed in more detail, several studies have shown that in spite of the presence of a selection of potential host plants, certain fungi only form mycorrhiza with particular hosts. Such “host preference” appears widespread in both EM (Kranabetter et al. 1999; Cullings et al. 2000; Kernaghan et al. 2003; Ishida et al. 2007; Tedersoo et al. 2007a, 2008a, 2010b, 2011; Morris et al. 2008, 2009; Cavender-Bares et al. 2009; Smith et al. 2009, 2011; Diédhiou et al. 2010; Wolfe and Pringle 2011) and arbuscular mycorrhizal (AM) systems (Helgason et al. 2002, 2007; Hart et al. 2003; Bever et al. 2009; Hausman and Hawkes 2009, 2010; Kiers et al. 2011; Davidson et al. 2011). Hart and Klironomos (2002) describe such preferences in AM systems as a type of “functional specificity” wherein fungi display differential benefit to neighboring plants. Recent research demonstrates that some hosts can selectively

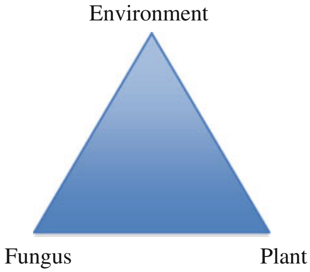

Fig. 1.2 The disease triangle. Compatible interactions between EM plants and fungi are influenced by the two symbionts (e.g., age of the seedling, carbon cost of the fungus, etc.) and by the environment. The environment includes the light environment, soil and nutrient type or availability (e.g., organic or inorganic N), as well as neighboring plant and fungal species in the networks

allocate photosynthate to a beneficial versus a non-beneficial fungus, and some fungi can discriminate among roots for carbon supply (Bever et al. 2009; Kiers et al. 2011). As we will discuss in more detail, these types of interactions and responses by fungi and plants associated with a mycelial network can significantly affect mycorrhizal community dynamics.

Early research on patterns of mycorrhiza specificity relied on associations of sporocarps (or spores for AM fungi) with particular plant hosts in nature or inoculation experiments such as the elegant pure culture syntheses of ectomycorrhiza by Melin (1922, 1923) or early pot studies by many researchers on arbuscular mycorrhiza. For mycorrhizal fungi that develop macroscopic reproductive structures (e.g. mushrooms and truffles) or easily retrievable spores (certain AM fungi), the resulting patterns of host-fungus associations provided valuable clues on mycorrhiza specificity, evolution, and host-fungus migration (Trappe 1962; Newton and Haigh 1998; Halling 2001; den Bakker et al. 2004; Vellinga et al. 2009; Wilson et al. 2012). Unfortunately not all mycorrhizal fungi produce showy and easily identified reproductive bodies, especially not in controlled settings, and field associations are not absolute proof of mycorrhizal relationships, particularly in stands composed of multiple host species.

The advent of PCR-based molecular techniques revolutionized our ability to identify plant and fungal symbionts on colonized roots, to derive phylogenetic relationships among mycorrhizal fungi, and thus to address concepts of mycorrhiza specificity with enhanced precision (reviewed in Horton and Bruns 2001; Peay et al. 2008). The patterns of presence and prevalence of multi-host fungi versus host specific fungi, or those showing host preference, have been fine-tuned with the application of molecular techniques in the field (Kennedy et al. 2003; Ishida et al. 2007; Twieg et al. 2007; Diédhiou et al. 2010; Smith et al. 2011; Polme et al. 2013; Roy et al. 2013). Molecular studies have also shed new light on the abilities of some fungi to form multiple types of mycorrhizae. For example, many EM fungi also form orchid, arbutoid, or monotropoid mycorrhizae (Taylor et al. 2002; Bidartondo et al. 2004), and some may even form ericoid mycorrhizae (Bergero et al. 2000; Allen et al. 2003; Villarreal-Ruiz et al. 2004; Grelet et al. 2009, 2010). Molecular studies of mycoheterotrophic plant roots have also revealed extreme fungal specificity and exploitive (parasitic) associations within mycorrhizal symbioses (Taylor et al. 2002; Bidartondo 2005). Molecular studies continue to provide a wealth of new information and approaches to determine the potential for linkage between neighboring plants, resulting in the formation of CMNs.

Many ecological and management implications flow from our understanding of CMNs as structured by mycorrhiza specificity processes and phenomena. Molina and Trappe (1982) first used "common mycelial networks" in a discussion of mycorrhiza specificity expressed by the arbutoid mycorrhizal plants *Arbutus menziesii* and *Arctostaphylos uva-ursi*; the authors hypothesized that these plants maintain EM fungus diversity in forest ecosystems following disturbance and benefit seedling establishment of later-seral Pinaceae because seedlings can exploit the mycorrhizal networks supported by these arbutoid plants. Similar examples of mycorrhiza specificity affecting formation and function of CMNs in diverse ecosystems abound and will be discussed later. The introduction of exotic, and potentially invasive, mycorrhizal fungi and plants worldwide is also influenced by compatible symbionts and mycorrhiza specificity processes (Vellinga et al. 2009; Nuñez et al. 2009; Dickie et al. 2010; Hynson et al. 2013; Karst et al. 2014; Hayward et al. 2015a, b). Similarly, as climate changes, the successful migration of plants and fungi into new habitats shaped by changing environmental conditions will be affected by compatibility of existing mycelial networks and the co-migration of compatible symbionts during migration.

We do not comprehensively review mycorrhiza specificity in this chapter; instead, we focus on what has been learned since the review by Molina et al. (1992). Our main goal is to provide a clear understanding of how mycorrhiza specificity influences the development and function of CMNs by addressing the following objectives: (1) refine a working lexicon of terms for mycorrhiza specificity research, (2) provide an updated overview of patterns of specificity seen in EM associations, and (3) exemplify the ecological consequences of how these specificity phenomena influence community dynamics, ecosystem resiliency, and the functions of CMNs. Given our expertise, we focus on EM symbioses but draw upon examples of other mycorrhiza types as appropriate.

1.2 The Lexicon

As ecologists we are acutely aware of the use and abuse of ecological terms (Tansley 1935), and those applicable to mycorrhiza specificity are no exception. In this section our objective is to clearly define our use of terms in this chapter. Some of the terms are drawn from the ecological literature, some from plant pathology, and some are unique to mycorrhizal symbioses. We provide definitions in Table 1.1, and elaborate on these in the following section.

Table 1.1 Definitions of terms used when discussing mycorrhiza specificity

Word or phrase	Definition
Symbiosis	Literally, living together. Can be a pathogenic, parasitic or mutualistic interaction
Mutualism	A symbiosis in which both organisms increase their fitness through the interaction. Increased uptake or allocation of resources, and improved growth are typically surrogates for fitness in mycorrhizal mutualisms
Fitness	The genetic contribution by an individual's descendants to future generations of a population. While biomass is often used as a proxy for fitness, it does not directly account for reproductive success
Mycorrhiza, mycorrhizas, mycorrhizae, mycorrhizal When to use these?	It is believed that the term mycorrhizae was first coined by A.B. Frank. He combined two Greek roots, mycor- for fungus and -rhiza for root (plant root). He used mycorrhiza for singular, mycorrhizae for plural, and most researchers followed that approach. But actually there was a problem. The—ae ending is Latin, and so Frank combined two Greek roots with a Latin ending. Many today argue for an English plural ending, so we get mycorrhizas. Neither uses a Greek ending, so neither is actually 'correct'.
	The use of the adjective mycorrhizal is perhaps more interesting (for those interested in this kind of thing!). What follows is a personal communication from Dr. Jim Trappe on whether to use mycorrhiza or mycorrhizal with specificity: 'Mycorrhiza' is a noun, but unlike most languages, English lets us use nouns as adjectives. When we do, always or maybe nearly always it's a short-handed way of saying the possessive case, i.e. 'mycorrhiza specificity' = 'of mycorrhiza' or 'of mycorrhizae', depending on the context. 'Mycorrhizal' is strictly an adjective, meaning the property of forming or being part of a mycorrhiza, e.g. 'a mycorrhizal host' or a 'mycorrhizal fungus'. Having counted how many angels can dance on the head of a pin, I pound my gavel on the judge's bench and pronounce: "specificity" cannot be mycorrhizal, that's like saying 'specificity forms a mycorrhiza' or 'specificity is a participant in forming a mycorrhiza'. 'Mycorrhiza specificity' means "specificity of mycorrhizae". This may not be strictly accurate, because we really mean host or fungus specificity, but in my opinion (that's what judges do, give opinions), the term implies specificity of either or both components of a 'mycorrhiza'
	Note from TRH: It seems to me that the issue is not whether to use mycorrhizal or mycorrhiza with specificity if both can connote an adjective and both suffer from the suggestion that specificity can form a mycorrhizal root which it cannot. We probably will continue to use mycorrhiza specificity (or mycorrhizal specificity) even though, as Judge Trappe suggests, we mean the specificity of the fungus and/or plant forming the mycorrhizal root tip. Note that the titles of multiple publications by Molina, Horton and Trappe in the literature citation list for this chapter used the –al form when referring to specificity, symbioses, inoculation, ecology and networks, none of which can be mycorrhizal according to judge Trappe! So much for clarity

(continued)

Table 1.1 (continued)

Word or phrase	Definition
Mycorrhiza specificity	An umbrella term that refers to the range of symbionts with which a fungus or plant develops a mycorrhizal symbiosis and the influences that contribute to the compatibility of the symbionts. Narrow range species necessarily associate with fewer symbiotic partners compared to broad range species, but we emphasize the phylogenetic breadth over richness
Mycorrhiza compatibility	The ability of a fungus and plant to form an anatomically defined mycorrhiza (Refer to Peterson et al. (2004) for anatomical definitions and images of the various mycorrhizal types)
Degree of mycorrhiza specificity	The breadth of taxonomic diversity with which a mycorrhizal species associates (synonymous with degree of host specificity)
Host range of the fungus:	Host range displays a continuum from narrow (associated with closely related hosts such as members of a single genus) to broad (associated with unrelated hosts such as both angiosperm and conifer species). Mycorrhizal fungi with narrow host ranges are often called “specialists” while those with diverse hosts are called “generalists.” Specialist and generalist are relative terms and should be carefully defined within the context of the study
Fungus range of the host:	The breadth of fungus taxonomic diversity with which a plant species associates. Analogous to host range, fungus range displays a continuum from narrow (fungal associates are closely related) to broad (fungal associates are a phylogenetically diverse group)
Fidelity to a mycorrhizal type	The ability of a plant or fungus to form one or more mycorrhizal types (type in this case refers to the anatomically defined categories of mycorrhiza)
Ecological specificity	The influence of biological or environmental factors on the ability of a plant and fungus to form a compatible mycorrhiza in soil. Based on the disease triangle in plant pathology
Host preference/selectivity	Consistent patterns of nonrandom assemblages between plant and fungal species are observed more or less frequently than expected by chance, despite an absence of compatibility limitations between the symbionts. The mechanisms behind these patterns are not well understood, including whether the plant or fungus or both control the association frequency
Host shift	An evolutionary process wherein a fungus colonizes a new plant species when its primary host species is going locally extinct or no longer available

1.2.1 Symbiosis

Frank originally coined the term “symbiotism” in 1885 (Trappe 2005) to encompass the full range of interspecific interactions from parasitism to mutualism. More recently symbiosis, a variation of the term coined by de Bary in 1879, is widely used almost synonymously with mutualism. We find Frank's original meaning better, in part because it allows for multiple outcomes along the parasitism—mutualism continuum.

1.2.2 Mutualism

Mutualisms are symbioses in which both organisms benefit from the interaction. Widespread examples include mycorrhizal plants and fungi, lichens and plant pollinator systems. An organism that is generally labeled as a mutualist in relation to a second organism may still reduce the growth or even fitness of the second organism under certain conditions, a feature of the mutualism-parasitism continuum noted in mycorrhizal symbioses (Johnson et al. 1997).

1.2.3 Fitness

The contribution of an individual's genotype to succeeding generations. While biomass and relative growth rate (RGR) may provide good proxies for fitness, they are not direct measures. As a result, a plant may sustain a negative RGR at the seedling stage as it allocates carbon to its mycorrhizal fungi while actually increasing its fitness through increased survival and reproductive output in the future (Stanley et al. 1993).

1.2.4 Mycorrhiza Specificity

Phylogenetic range of the symbionts known to form mycorrhizal associations with a particular plant or fungal species. This general term takes neither a fungus- or plant-centric view. Mycorrhiza specificity may be narrow, as in the restriction of *Suillus* species to members of Pinaceae (Kretzer et al. 1996), or broad as in the 2000 species of EM fungi known to associate with Douglas-fir (*Pseudotsuga menziesii*, Trappe 1977). This umbrella term serves as a construct to discuss various specificity phenomena expressed in mycorrhizal symbioses.

1.2.5 Mycorrhiza Compatibility

The ability of a fungus and plant to form an anatomically defined mycorrhiza. This definition does not necessitate having data on the physiological nature of the symbiosis or "functional compatibility" as defined by Gianinazzi-Pearson and Gianinazzi (1983), i.e. physiological exchange of materials that point to a mutualistic symbiosis.

Given that the functional nature of mycorrhizal interactions varies tremendously between different plant and fungus associations (from one-sided parasitism to obligate mutualism), and that it is difficult to measure functional interactions, we use an anatomical definition of compatibility. Anatomically, the arbuscule (AM), Hartig net (EM), coil (ericoid, arbutoid, AM), hyphal peg (monotropoid), and peloton (orchidoid) are sites of nutrient transfer that we consider hallmarks of compatible associations. There may also be indications of incompatible associations, such as cortical cell disruption and phenolic compounds in colonized plant roots. The fact that hyphal cell disruption occurs in monotropoid hyphal pegs and orchidoid pelotons is an indication that these associations may be closer to, if not at, the parasitic end of the mutualism-parasitism continuum. We recognize that physiological interactions may be integral to the expression of mycorrhiza specificity phenomena, but leave functional aspects to a more thorough taxonomic survey based on experimental testing and genome surveys of functional genes.

1.2.6 Degree of Mycorrhiza Specificity

Prior to the use of extensive morphotyping in concert with molecular tools, the degree of mycorrhiza specificity in EM associations was based either on sporocarp-host observations, visually linking mycelium from sporocarps to EM roots of hosts in the field, or on pure culture synthesis experiments in the laboratory. The application of molecular tools on field-collected ectomycorrhizal root tips has provided greater data with more precision regarding fungal identity and the ability to test many of the assumptions and hypotheses put forth by earlier methods. Knowledge on specificity patterns represents hypotheses that are necessarily upheld or modified as new data are generated.

Host range of the fungus: Molina et al. (1992) described how EM fungi associate with host species along a spectrum from narrow to broad, and, for simplicity, divided the spectrum into three categories: narrow host range (restricted to a single host species or genus), intermediate host range (restricted to a host family, or a single taxonomic grouping, such as conifers or angiosperms), and broad host range (mostly unrestricted, associated with many host families, including both conifer and angiosperm). Species in the hypogeous EM genus *Rhizopogon* are classic examples that express primarily narrow specificity, associating with single genera within Pinaceae (e.g., *R. vinicolor* and *Pseudotsuga*); some *Rhizopogon* species, however, are intermediate and associate with several host genera within Pinaceae (e.g., *R. salebrosus*) (Molina et al. 1999). *Cenococcum geophilum*, with its cosmopolitan range and association with most EM hosts, exemplifies a broad host range EM fungus. Although these terms have been used in several publications, the terms “specialists” and “generalists” have proven more common as they are used in other ecological contexts.

These are all relative terms, however, and require definition within the context of the study, e.g., *Quercus* specialist, Fagaceae specialist, or angiosperm specialist.

Alternatively, one may directly state the degree of host restriction such as being *Quercus* specific, Fagaceae specific, or angiosperm specific.

"Multi-host fungus" is another commonly used phrase in EM fungal community studies in stands of mixed hosts and reflects the observed host range in that particular location. "Multi-host" is also a relative term that requires careful definition within the context of the study or when comparing results from different studies. For example, if one examines a stand with three genera of Pinaceae (e.g., *Pinus*, *Picea*, *Tsuga*) and three genera of angiosperms from two families (e.g., *Quercus*, *Betula*, *Fagus*), fungi that form ectomycorrhiza with all three Pinaceae hosts, all three angiosperm hosts, or a combination of Pinaceae and angiosperm hosts would all be considered "multi-host" fungi, yet could differ significantly in their host ranges and thus mycorrhiza specificity. Similarly, all "generalists" are not the same. For instance, although Wolfe and Pringle (2011) found that the EM fungus *Amanita phalloides* expresses broad compatibility with new hosts since it was introduced into North America, they did not consider it a true "generalist", because it did not associate with all EM hosts within its new range and showed strong host preferences in different locations. It is also important to keep in mind that genetic data has shown that some generalists are actually species complexes with individual species showing a higher degree of specialization (ecological or plant host) than expected based on a morphological species concept (Martin et al. 2002, 2008; Douhan et al. 2007; Geml et al. 2008).

Fungus range of the host: Ectomycorrizal hosts differ in the phylogenetic breadth of associated fungi. Molina et al. (1992) termed this fungus specificity phenomenon "host receptivity," defined simply as the number of fungal species associated with a host. Note that this is without reference to the phylogenetic breadth of the associates. Host receptivity has not been widely used since the 1992 paper. To make the fungus range of the host analogous to the host range of the fungus, we suggest using the degree of phylogenetic breadth of the fungi associated with hosts ranging from narrow (as seen in *Pterospora andromedea*, which only associates with several closely related *Rhizopogon* spp.) to broad (as seen in *Pseudotsuga menziesii*, known to associate with thousands of fungal species from numerous and distantly related phylogenetic groups). As noted for fungal host range, it is best to define the context when referring to the fungus range of the host.

1.2.7 Symbiont Fidelity to a Mycorrhiza Type

The term "fidelity" is used in early plant community ecology literature in reference to the constancy a plant species exhibits in a particular community association. We use it similarly but in reference to whether plant or fungal species are constant in the type of mycorrhiza they form. It is a valuable concept in describing mycorrhiza specificity phenomena, because it implies wide ranges of compatibility among diverse plants and fungi and indicates the potential for CMNs among plants. Most mycorrhizal plants and fungi express fidelity to one mycorrhiza type. There are many exceptions, however, and molecular tools have raised several questions in this regard. Well known exceptions include a large group of hosts that form both ectomycorrhizae and arbuscular mycorrhizae (e.g., several species in Fagaceae, *Eucalyptus*, *Populus*, *Salix*); these hosts often form arbuscular mycorrhiza early as seedlings but become predominately EM as mature plants (see Molina et al. 1992; Brundrett 2004; Smith and Read 2008 for lists of these plants and more through discussion). AM colonization has also been noted in typically non-AM hosts, such as the *Pseudotsuga* (Cázares and Smith 1995), and *Pinus* (Horton et al. 1999). Koske et al. (1990) reported AM colonization along with ericoid mycorrhiza in several Hawaiian Ericaceae. We will probably continue to discover more incidences of AM colonization of typically EM or ericoid hosts as we explore this phenomenon further, and it remains to be seen whether these result from opportunistic colonization in roots lacking a fungal mantle with no obvious fitness enhancement to the plants (perhaps following disturbance as seen in Horton et al. 1999) or functional mutualisms as evidenced by increased P uptake with AM colonization in *Pseudotsuga* (Cázares and Smith 1995).

Molecular tools have shed considerable new light on the interactions of EM fungi with arbutoid hosts, such as *Arctostaphylos* spp. (covered below), and mycoheterotrophic plants in Orchidaceae and Ericaceae. EM fungi of forest trees are the main mycobionts of mycoheterotrophic plants, and mycotrophic plants typically have a very narrow fungus range such as a single species or a group of closely related species (Taylor et al. 2002; Bidartondo 2005). Although debate continues on whether these are mutualistic or parasitic symbioses, they are anatomically referred to as mycorrhiza (Peterson et al. 2004), and certainly lie within the parasitism-mutualism continuum recognized for all mycorrhizal symbioses (Johnson et al. 1997). Several recent molecular studies have also shown that some EM fungi can form both ectomycorrhiza and ericoid mycorrhiza (Bergero et al. 2000; Allen et al. 2003; Villarreal-Ruiz et al. 2004; Grelet et al. 2009, 2010). Such findings led Vrålstad (2004) to entertain the possibility of EM and ericoid fungi operating within a "common guild" and potentially developing CMNs that may yield ecologically significant interactions between overstory EM trees and understory Ericaceae.

Molecular studies and further root sampling worldwide will continue to clarify the lines of mycorrhiza fidelity. For example, the ericoid mycorrhizal fungus *Rhizocyphus ericae* is widespread in the leafy liverwort *Cephaloziella various* in Antarctica, and an isolate from the liverwort formed typical ericoid mycorrhizae with *Vaccinium macrocarpon* seedlings upon inoculation (Upson et al. 2007). Several fungi that form ericoid mycorrhizae with *Woolsia pungens* were also isolated from 17 plants in a southeastern Australian forest (Chambers et al. 2008). Members of the Sebeniales also blur the fidelity line, as several species are involved in ecto-, orchid, and ericoid mycorrhiza (Selosse et al. 2002a, b; Allen et al. 2003; Urban et al. 2003; Setaro et al. 2006). These patterns reveal an interesting line of research: who is in control of a compatible interaction and characteristic anatomical features of each mycorrhizal type, the plant, fungus, or both?

1.2.8 Ecological Specificity

Harley and Smith (1983) used this concept in reference to the ability of plants and fungi to express different mycorrhiza compatibility under natural conditions compared to laboratory conditions, such as pure culture syntheses, and it has its roots in the disease triangle (Fig. 1.2).

Molina et al. (1992) expanded the definition to include the influence of biological or environmental factors on the ability of a plant and fungus to form a compatible interaction in soil. This concept emphasizes the point that factors beyond potential genetic compatibility of host and fungus can influence whether mycorrhizas develop under natural conditions, as indicated in the disease triangle. For mycorrhizal networks, the environment includes neighboring plants that can influence whether a particular fungus forms mycorrhiza with other co-occurring plant species.

1.2.9 Host Preference and Selectivity

In field studies with experimental designs that allow researchers to rule out random affects, consistent patterns of associations between plant and fungal species are observed more or less frequently than expected by chance, despite an absence of compatibility limitations between the symbionts. Further, in field studies of EM fungal communities involving multiple neighboring host species, some fungi occur more frequently on one host compared to a different neighboring host species (Kranabetter et al. 1999; Cullings et al. 2000; Kernaghan et al. 2003; Ishida et al. 2007; Tedersoo et al. 2007a, 2008a, 2010b, 2011; Morris et al. 2008, 2009; Cavender-Bares et al. 2009; Smith et al. 2009, 2011; Diédhiou et al. 2010; Wolfe and Pringle 2011). This phenomenon is called "host preference" (or selectivity) and is widespread in EM and AM systems (several detailed examples are provided in a later section). The mechanisms and ecological processes that yield patterns of host preference are largely unknown but likely include a complex of factors, such as competitive interactions among fungi, phylogenetic and physiological differences among hosts, and preferential allocation of resources between symbionts (Dickie 2007; Bever et al. 2009; Tedersoo et al. 2010a; Kiers et al. 2011). Host preference can influence fungal and plant community dynamics, as well as the structure and function of CMNs.

1.2.10 Host Shift

Host shift (or switch) is viewed in the pathology literature as an evolutionary process wherein a fungus becomes relatively more abundant on (shifts to) a new host when the original primary host is declining or no longer available. This allows the fungus to persist in its current range or even expand its range. The concept has also been applied in the evolution of EM fungi. As examples, Wilson et al. (2012) provided evidence for host shifts of *Scleroderma* species from ancestral Pinaceae to various angiosperms, as well as between angiosperms (Myrtaceae and Fagaceae). Within EM *Leccinum*, specific to *Betula* hosts, den Bakker et al. (2004) describe likely host shifts from *Betula* to *Populus* to Arbutoidae (that is, associations with Betulaceae to Salicaceae to subfamily Arbutoideae in Ericaceae). Given the expression of strong host specificity by several linages of EM fungi associated with *Alnus*, Tedersoo et al. (2009) suggest "multiple, independent host shifts". An exact event of host shift is difficult to distinguish, because the process is likely to unfold over a long period of time wherein the fungus may associate with both hosts until the original host disappears. An exception may be when fungi are introduced into new locations far distant from their original hosts. For example, Wolfe and Pringle (2011) note the shift by *Amanita phalloides* to several EM hosts when introduced into North America, an ability likely made possible by ancestral compatibilities with a diverse range of EM hosts in Europe.

Host shift has also been used to describe the movement of native EM fungi onto introduced hosts (Tedersoo et al. 2007b). However, we do not support this use of the term because this does not describe an evolutionary process, and the original local hosts are present and not declining. Cases of introduced hosts forming ectomycorrhiza with native EM simply represent an expansion of the host range for those fungi, again likely to be brought about by broad ancestral host compatibility. For example, Bahram et al. (2013) found that several EM fungi associated with native Fagaceae and Betulaceae in Iran formed ectomycorrhiza on introduced *Pinus sylvestris*. They hypothesized that, although *P. sylvestris* is not native to Iran, it occurs sympatrically with Fagaceae and Betulaceae in Europe, and compatibility of fungi associated with native angiosperm hosts with introduced pines in Iran may reflect ancestral EM fungus compatibility with Pinaceae.

1.3 Ecological Specificity and Host Preference

How do biotic and abiotic factors influence fungal and plant community dynamics and the role of mycorrhiza specificity phenomena? Among biotic factors, neighboring plants can exert significant effects on how fungi develop mycorrhizae within a mixture of potential hosts. For example, when various fungus and host species are grown in plant mixture and monoculture experiments, a fungus may only develop mycorrhizae on a particular host in specific treatment combinations, or differ in the degree of colonization depending on the presence of different hosts. Massicotte et al. (1994) and Molina et al. (1997) found that following spore inoculation, several *Rhizopogon* species (Pinaceae specialists) formed arbutoid mycorrhizae with arbutoid hosts (*Arbutus* or *Arctostaphylos* spp.) when grown in bioassays with their typical Pinaceae host species, but not when grown in an arbutoid host monoculture. Similarly, Douglas-fir specialist *Rhizopogon* species can also colonize western hemlock (*Tsuga heterophylla*) seedlings when grown in dual host bioassays with Douglas-fir seedlings (Smith et al. 1995). Massicotte et al. (1999) grew several mixtures and monocultures of EM hosts in forest soil and found that some EM fungi only formed ectomycorrhizae with particular hosts in mixed cultures. Again, this included the colonization of *Arbutus menziesii* by Pinaceae specialists when grown in host mixtures. In a greenhouse forest soil bioassay that examined shared compatibility between Douglas-fir and *Betula papyrifera*, Simard et al. (1997a) found that Douglas-fir only formed ectomycorrhizae with *Tuber* spp. when grown in mixture with *Betula*, and the mixture treatment also affected frequency and abundance of retrieved morphotypes.

Host neighbor effects also occur under natural field conditions. Jones et al. (1997) found that the evenness of the EM fungal community on Douglas-fir was greatest when seedlings were planted in mixture with *Betula papyrifera* seedlings in clearcuts, although overall richness of EM types was not affected. Nara (2006a, b) detected the *Larix* specialist *Suillus larcinus* on a *Betula* seedling when growing next to a *Larix* sapling. Similarly, Horton (unpublished data) found the *Arctostaphylos* specialist *Leccinum manzanitae* on neighboring *Pinus contorta* roots in a sand dune habitat, corroborating earlier pure culture synthesis results of Molina and Trappe (1982). Presence of ericaceous plants can influence the EM fungal community of forest trees. Kohout et al. (2011) report that neighboring *Vaccinium* significantly promoted abundance of *Rhizopogon salebrosus* and inhibited *Thelephora terrestris* on pine; *Wilcoxina* only occurred on pine when *Vaccinium* was present.

Abiotic factors such as soil composition, chemistry, and soil moisture can influence the growth and establishment of different EM fungal species (Baar and de Vries 1995; Koide et al. 1998; Conn and Dighton 2000; Dighton et al. 2000; Cullings et al. 2003; Cavender-Bares et al. 2009). For example, the litter of some plants and resulting decomposition products may influence the EM fungal community found on adjacent hosts. Aponte et al. (2010) examined the EM fungal community of two co-occurring Mediterranean oaks, and of 69 OTUs (operational taxonomic units) recovered, only 13 were found on both oak species; 29 were exclusive to *Quercus canariensis* and 27 only on *Q. suber*. They found that Ca content was highest under the winter deciduous *Q. canariensis* and that differences in EM fungal communities were correlated with Ca content in the soil. Morris et al. (2009) also suggest that differences in litter quality affected host preferences between two *Quercus* species in a tropical cloud forest in southern Mexico.

Most field reports of ecological specificity phenomena are based on observational data of host-fungus associations and frequency of occurrence. Tests of hypotheses regarding expression of ecological specificity are rare and needed to improve our understanding of the factors influencing mycorrhiza specificity. Hayward and Horton (2012), for example, tested whether the host specific nature of EM fungi associated with *Pisonia grandis* on the Pacific island of Rota was due to soil or host factors. *Pisonia grandis* associates with a restrictive set of EM fungi and throughout much of its range occurs in habitats rich in guano. Cairney et al. (1994), Chambers et al. (2005), and Suvi et al. (2010) suggest that this unique habitat has shaped the EM fungal associates of *P. grandis*, i.e., an expression of ecological specificity. Hayward and Horton (2012) found that *P. grandis* formed ectomycorrhizae with the same set of EM fungi on guano rich and guano poor habitats, and that several EM fungi on neighboring EM hosts (*Instia bijuga* and *Casaurina equisitifolia*) were not observed with *P. grandis*. They concluded that edaphic factors (i.e., ecological specificity phenomena) did not explain the host specialist fungal associations of *P. grandis*, and that specificity may be due to derived or ancestral characters within *Pisonia*.

1.3.1 Host Preference

When Newton (1991) grew *Quercus robur* and *Betula pendula* seedlings in a variety of soils in England, he found dissimilar EM fungal communities; although the two most common fungi were found on each host, they differed in abundance. He stated that this type of "ecological specificity" accounted for the distinct EM fungal communities of oak and birch, and should more accurately be termed "host preference". With the advent of molecular tools to identify host-fungus associations of field collected roots and statistical testing for host association, several field studies have subsequently demonstrated the widespread prevalence of host preference in EM systems (Kranabetter et al. 1999; Cullings et al. 2000; Kernaghan et al. 2003; Ishida et al. 2007; Tedersoo et al. 2007a, 2008a, 2010b, 2011; Morris et al. 2008, 2009; Cavender-Bares et al. 2009; Smith et al. 2009, 2011; Diédhiou et al. 2010; Wolfe and Pringle 2011). Given the difficulty of demonstrating absolute host-fungus specificity in the field (Taylor 2002; Dickie 2007; Tedersoo et al. 2010b) and the widespread nature of host preference, Dickie and Moyerson (2008) state that host preference (rather than host specificity) may be considered "more the rule rather than the exception" in diverse EM fungal communities. Although host preference is often displayed among taxonomically distant hosts (e.g., angiosperms versus conifers) or at the family level, it also occurs between closely related taxa such as co-occurring *Quercus* species (Morris et al. 2008, 2009; Cavender-Bares et al. 2009; Aponte et al. 2010).

Although widespread, the degree of host preference exhibited in different EM fungal communities can vary from high to low. For example, in a neotropical forest of the western Amazonia, Tedersoo et al. (2010b) found that two thirds of the EM fungi preferred one of three hosts examined, and four of the six most frequent EM fungi showed statistically significant host preference at the host genus level but not at the species level. Tedersoo et al. (2008a) similarly found strong host preference of EM fungi in a Tasmanian sclerophyll forest. In a mixed boreal forest in Canada, Kernaghan et al. (2003) found dissimilar EM fungal communities between angiosperm and conifer hosts, with some fungal species showing a preference for *Abies/Picea* and others for *Populus/Betula*; overall, 30 % of the most abundant EM fungi expressed host specificity and 25 % expressed various levels of host preference. Similarly, Ishida et al. (2007) showed a high degree of host specificity and preference among eight EM hosts in a mixed conifer-broadleaf forest in Japan; host preference was most common at the host family level. In contrast, Tedersoo et al. (2011) found low levels of host preference in wooded savannahs and rain forests of Africa, while Smith et al. (2013) report low levels of host preference between distantly related ectomycorrhizal hosts in neotropical highlands of the Guiana shield in Guyana. Smith et al. (2011) detected no host preference for EM fungi associated with three co-occurring leguminous host trees in a neotropical rainforest (a sharp difference to results of Tedersoo et al. (2010b) in neotropical western Amazonia). EM fungi that display host preference are not necessarily restricted to those found in low abundance or with a restricted host range. Several studies show that many of the most common fungi in EM fungal communities, including many multi-host fungi, can display host preference (Kranabetter et al. 1999; Kernaghan et al. 2003; Tedersoo et al. 2008a, 2010b). As with general specificity phenomena, host preference is likely to be influenced by environmental conditions. Also, as nicely argued in Taylor (2002), the typically high species richness in EM fungal communities on root tips and their cryptic nature makes it very difficult to sample the number of root tips needed to adequately sample the mycorrhizal root types of all the plant species in a plot. This issue has implications for our ability to fully document host preference, especially for species that are observed on a limited number of samples. Further, environmental factors that favors both host and fungal species may give a false impression of host preference at the root tip level. It is critically important that future field studies use robust sampling methods that provide strong statistical inferences regarding the interpretation of host preference patterns.

Many factors determine how an EM fungus responds to new hosts when introduced into a novel geographic range, including the degree of host specificity displayed in the native range (i.e. generalist to specialist tendencies), compatibility with newly encountered hosts, niche availability, interactions with the native fungal flora, soil conditions and other biotic factors (Molina et al. 1992; Vellinga et al. 2009; Wolfe and Pringle 2011). The introduction and spread of *Amanita phalloides* into North America (Wolfe and Pringle 2011) provides a robust example of how these factors interact with relevance to ecological specificity and host preference. Wolfe and Pringle (2011) conducted an extensive survey of the geographic distribution of *A. phalloides* across its native range in Europe and expanded range in N. America, and tested for host selectivity and niche shifts. In Europe *A. phalloides* primarily associates with *Quercus* and other Fagaceae, but rarely with Pinaceae. In N. America, *A. phalloides* associates primarily with Pinaceae in the East Coast, rarely spreading into natural forests. On the West Coast it is more widespread, occurs in native forests, and as it is in Europe, is most commonly associated with *Quercus*. Although the 11 documented novel host associations (host shifts) in N. America is indicative of broad host compatibility, the authors did not consider *A. phalloides* a true “generalist.” Instead, they state that *A. phalloides* exhibits “geographically structured host specificity.” In California, for example, *A. phalloides* “selectively” associates with

Quercus agrifolia, an evergreen oak, and the distribution of the fungus strongly correlates with the distribution of this oak species. Wolfe and Pringle (2011) suggest that association with *Q. agrifolia* may provide a competitive advantage of *A. phalloides* over the local EM fungal flora and allow it to persist and spread, as an outcome of ecological specificity and host preference. They conclude by stating "specificity in local habitats can influence the success of introduced mutualist species even when the species otherwise appears a generalist."

A complex of factors contribute to the expression of host preferences and differences among hosts and fungi. Tedersoo et al. (2010b) list historical factors, specialized habitat, partial autotrophy, as well as phylogenetic and physiological differences among hosts as important contributors to host preference expression. In the absence of absolute host specificity as determined by genetic factors, Dickie (2007) hypothesizes that host preference is in essence an expression of "realized niche" that may be driven by competitive interactions among the EM fungi in the community, or alternatively, by direct host selection of a particular fungus, i.e., that a host selectively provides resources (e.g. photosynthates) to a preferred fungal species that is highly beneficial to the host. Discussion of "partner choice" has received substantial attention in the recent AM literature, including how such host-fungus interactions may yield significant host preference and stability to mycorrhizal symbioses (Kiers and van der Heiden 2006; Kiers et al. 2011; Bever et al. 2009). Bever et al. (2009) demonstrated preferential allocation of photosynthate by *Allium* to a mutualistic *Glomus* species rather than non-beneficial *Gigaspora margarita* when the plant was mycorrhizal with each fungus growing in separate split root compartments; the preferential C allocation also increased fitness (spore number) of *Glomus* under these growth conditions. Kiers et al. (2011) also report how significant host preference between *Medicago truncatula* and three *Glomus* species resulted in both preferential carbon allocation to the most beneficial fungus and the ability of the cooperative fungi to transfer more P to those roots providing greatest access to photosynthate (i.e. that fungi can discriminate among carbon supply by different hosts). Fungi were not separated into compartments in these experiments. Kiers et al. (2011) suggest that such reciprocal rewards in mycorrhizal host-fungus interactions contribute to stability of the mycorrhizal mutualism.

Selective allocation of resources to differentially beneficial fungi in EM systems has yet to be demonstrated. Some host specific fungi, however, can provide greater benefit to their specific host than generalist fungi. For example, Gorissen and Kuyper (2000) found that pine seedlings inoculated with the host-specialist fungus *Suillis bovinus* took up more nitrogen than seedlings inoculated with the host generalist *Laccaria bicolor*. Indirect evidence for increased allocation of N by host specialist fungi compared to generalists is also supported by higher $^{15}N/^{14}N$ ratios among host specialist fungi (Taylor et al. 2003; Hobbie et al. 2005). Chu-Chou and Grace (1985) found that the pine specialists *Rhizopogon rubesens* and *R. luteolus* were more effective symbionts for *Pinus radiata* than the host generalists *Laccaria laccata* or *Hebeloma crustuliniforme*. *Rhizopogon vinicolor* provided greater drought tolerance to its specific host Douglas-fir than the generalists *Laccaria laccata* or *Pisolithus tinctorius* (Parke et al. 1983) and stimulated higher photosynthetic rates than *L. laccata* or *H. crustulinforme* (Dosskey et al. 1990). Further experimentation in all mycorrhizal systems is needed to explore the mechanisms for expression of mycorrhiza specificity, particularly the influence of resource allocation between the symbionts, and how this affects formation and function of CMNs.

In summary, the relevance of host specificity, ecological specificity, and host preference can be substantial in diverse ecosystems and influence the formation and function of CMNs. Host specificity and preferences affect the structure of plant and fungal communities and successional dynamics (see section on plant community dynamics). Several studies show that increased host diversity on the landscape is often accompanied by higher levels of host specificity and higher fungal diversity than in locations with low EM host diversity (Newton and Haigh 1998; Kernaghan et al. 2003; Kernaghan 2005; Debellis et al. 2006; Ishida et al. 2007; Dickie 2007; Tedersoo et al. 2012). Host specificity and preference create unique niches at the order of host roots, providing opportunities for multiple mycorrhizal fungi to persist and function, and also affect resource partitioning among sympatric hosts (Dickie 2007; Ishida et al. 2007; Peay et al. 2008; Tedersoo et al. 2008b; Horton et al. 2013). Host specificity and preference will also affect natural migration or exotic introductions of fungi, influencing their ability to form mycorrhiza with potential compatible hosts, and as such influence invasive potential (Karst et al. 2014; Vellinga et al. 2009; Wolfe and Pringle 2011). Finally, in an evolutionary context, potential expression of host specificity or preference may influence host shifts and thus contribute to fungal speciation (Kretzer et al. 1996; Halling 2001; den Bakker et al. 2004; Wilson et al. 2012).

1.4 Influence of Mycorrhiza Specificity on Plant Community Dynamics and Ecosystem Resiliency

Numerous reviews highlight that different plant species, often from different families, can be colonized by the same EM fungus when grown together in experimental bioassays (pot cultures) or naturally in the field (Table 1.2; Newman 1988; Simard and Durall 2004; Selosse et al. 2006). This potential is provided by the often abundant and dominant presence of fungal species with intermediate to broad host-ranges. Such overlap in host compatibilities and formation of functioning CMNs between diverse hosts can strongly influence plant community dynamics during primary and secondary plant succession, and overall ecosystem resiliency (Molina and Trappe 1982; Perry et al. 1989; Molina et al. 1992; Horton and van der Heijden 2008; van der Heijden and Horton 2009; Kennedy et al. 2012; Nara, Chap. 6, this volume). During plant succession many early seral plant species act as “legacy” or “refuge” plants wherein they establish (in primary succession; Nara 2006a, b, this volume) or maintain (in secondary succession; Horton et al. 1999) a diversity of EM fungi that will benefit later seral plants. Maintenance of EM fungal biodiversity and functional diversity creates a positive feedback beneficial to ecosystem recovery and resilience (Perry et al. 1989; Molina et al. 1992). Below we provide one robust example of legacy plant function and facilitation of plant community dynamics via potential ectomycorrhizal CMNs from our work with arbutoid mycorrhizal hosts in Western North America, and then briefly discuss other examples from diverse ecosystems worldwide (refer to Table 1.2 for additional details on the degree of overlap between hosts and experimental conditions of the exemplified studies).

While the examples below from different EM plant communities illustrate potential aspects of facilitation via CMNs, additional field studies are needed to add support for these ideas with clear empirical evidence. Attention is particularly needed on the functional differences between dominant generalist EM fungi and those fungi that show different levels of host preference or specificity.

1.4.1 Arbutoid Mycorrhizal Legacies in Secondary Succession

Research on arbutoid mycorrhizal host genera *Arbutus* and *Arctostaphylos* in the frequently disturbed Pinaceae forests of the western USA exemplifies the role mycorrhizal networks can play in plant community dynamics. Arbutoid hosts have a broad receptivity towards a diversity of EM fungi (Zak 1976a, b), leading Molina and Trappe (1982) to hypothesize that the plants maintain a reservoir of diverse EM fungi through disturbance events that support the establishment of later successional Pinaceae. Amaranthus and Perry (1989) and Borchers and Perry (1990) demonstrated a positive benefit in ectomycorrhiza formation and growth of *Pseudotsuga menziesii* (Douglas-fir) seedlings when inoculated with soil taken from beneath *Arbutus menziesii*. When seedlings of *A. menziesii* were grown in multispecies, pot cultures of Douglas-fir, grand fir (*Abies grandes*), and ponderosa pine (*Pinus ponderosa*) containing soil from a mature mixed evergreen forest, they developed seven EM morphotypes, and shared six of these with grand fir and ponderosa pine, and five with Douglas-fir (Massicotte et al. 1999). Notably, one of the fungi shared with *Arbutus* was a *Rhizopogon* sp., a Pinaceae specialist. Horton et al. (1999) were the first to investigate the facilitating nature of *Arctostaphylos glandulosa* associated EM networks for Douglas-fir seedlings. Douglas-fir established significantly better under *Arctostaphylos* compared to under the AM *Adenostoma fasciculatum* even though most environmental factors were conducive for Douglas-fir establishment under *Adenostoma*. They found that 17 of the 24 EM fungi colonizing Douglas-fir seedlings growing within the *Arctostaphylos* patches were also found on *Arctostaphylos*, and 49 % of the Douglas-fir EM root biomass associated with fungi also observed on *Arctostaphylos* roots in the same soil core. The authors hypothesized that Douglas-fir establishment in *Arctostaphylos* was likely to be facilitated via the EM fungi supported by *Arctostaphylos*.

Table 1.2 Context of ectomycorrhizal fungus colonization of multiple host species in diverse laboratory and field settings

Hosts	Overlap in EM Fungi	Methodology	Citation
Arbutus menziesii, *Arctostaphylos uva-ursi*, Pinaceae	30 species on arbutoid and Pinaceae	Pure culture synthesis	Zak (1976a, b) and Molina and Trappe (1982)
Arbutus menziesii, *Pseudotsuga menziesii*, *Abies grandis*, *Pinus ponderosa*	6 EMF on *Arbutus/Abies/Pinus* 5 EMF on *Arbutus/Pseudotsuga*	Soil bioassays/morphotype ID	Massicotte et al. (1994)
Arctostaphylos uva-ursi, *Pinus resinosa*	5 EMF on both hosts	Field EM roots/morphotype ID	Visser (1995)
Tsuga heterophylla, *Pseudotsuga menziesii*	11 EMF on both, one *Pseudotsuga* specialist observed on *Tsuga*	Soil bioassay/morphotype ID	Smith et al. (1995)
Pseudotsuga menziesii, *Betula papyrifera*	91 % of Betula and 56 % of *Pseudotsuga* EM morphotypes were on both hosts	Field EM roots/morphotype ID	Jones et al. (1997)
Pseudotsuga menziesii, *Betula papyrifera*	7 of 11 EMF on both hosts	Soil bioassay/morphotype ID	Simard et al. (1997a)
Pseudotsuga menziesii, *Pinus muricata*	12 of 16 EMF on both hosts	Field EM roots/molecular ID	Horton and Bruns (1998)
Arctostaphylos glandulsa, *Pseudotsuga menziesii*	17 of 24 EMF observed on *Pseudotsuga* also observed on *Arctostaphylos*	Field EM roots/molecular ID	Horton et al. (1999)
Lithocarpus densifolia, *Pseudotsuga menziesii*, *Abies grandis*, *Pinus ponderosa*	*Lithocarpus* showed 50 % overlap with Pinaceae EMF	Soil bioassay/morphotype ID	Massicotte et al. (1999)
Pinus contorta, *Picea glauca*, *Abies lasiocarpa*	74 EMF, 35 on all three hosts	Field EM roots/morphotype ID	Kranabetter et al. (1999)
Pinus contorta, *Picea engelmannii*	28 EMF, 21 on both hosts, 5 specific to *Picea*, none specific to *Pinus*	Field EM roots/molecular ID	Cullings et al. (2000)
Arctostaphylos uva-ursi, *Pseudotsuga menziesii*	17 morphotypes on *Pseudotsuga*, 14 morphotypes on *Arctostaphylos*, 10 EMF morphotypes (6 confirmed with RFLP typing) found on both	Field EM roots/morphotype and molecular ID	Hagerman et al. (2001)

(continued)

Table 1.2 (continued)

Hosts	Overlap in EM Fungi	Methodology	Citation
Lithocarpus densiflora, *Pseudotsuga menziesii*	56 EMF, 17 on both hosts	Field EM roots/molecular ID	Kennedy et al. (2003)
Helianthemum bicknellii, *Quercus spp/Q.macrocarpa*	8 EMF on *Helianthemum*, 7 of which also on *Quercus*	Field EM roots/molecular ID	Dickie et al. (2004)
Arbutus unedo, *Quercus ilex*	46 RFLP types on *A. unedo* 18 RFLP types also on *Quercus*	Field EM roots/molecular ID	Richard et al. (2005)
Tsuga heterophylla, *Pseudotsuga menziesii*	55 % overlap in early successional setting 14 % overlap in late successional setting	Field EM roots/molecular ID	Horton et al. (2005)
Cistus landanifer, *Pinus pinaster*	30 EMF with *Cistus*, many known *Pinus* associates	Fruitbody occurrence	Martin-Pinto et al. (2006)
Betula papyrifera, *Pseudotsuga menziesii*	105 EMF, 42 on both hosts, 23 only on *Pseudotsuga*, 40 only on *Betula*	Field EM roots/molecular ID	Twieg et al. (2007)
Betulaceae, Fagaceae, Pinaceae	14 EMF on only one host family, 37 EMF on both conifer and broadleaf host, 19 EMF on all three families, 6 EMF on Pinaceae and Betulaceae, 12 EMF on Pinaceae and Fagaceae 24 EMF on Betulaceae and Fagaceae	Field EM roots/molecular ID	Ishida et al. (2007)
Arbutus menziesii, *Pseudotsuga menziesii*, *Pinus* spp.	Study 1: 126 EMF on *Arbutus*, 17 also with Pseudotsuga or *Pinus* Study 2: 82 EMF, 25 on *Arbutus* and *Pseudotsoga*	Field EM roots/molecular ID	Kennedy et al. (2012)
Pterospora andromedea, *Pinus strobus*	Numerous EMF on *Pinus*, 1 *Rhizopogon* on both hosts	Field EM roots and bioassay/molecular ID	Hazard et al. (2012)
Pakaraimaea dipterocarpacea, *Dicymbe jenmanii*	16 of 52 OTUs shared, 13 of the 17 most common shared	Field EM roots/molecular ID	Smith et al. (2013)

(continued)

Table 1.2 (continued)

Hosts	Overlap in EM Fungi	Methodology	Citation
Castanea dentata, 8 other EM hosts in Fagaceae, Pinaceae and Betulaceae	71 RFLP types (EMF) with 41 found only on a single host, 22 of which were observed on a single root tip. *Castanea* was colonized by 24 EMF also associated with *Quercus rubra*, 7 EMF also associated with *Fagus grandifolia*, 6 EMF also with *Quercus alba, 4 EMF also with Betula lenta, 2 each with Ostrya virginiana*, *Tusga canadensis*, *and Pinus strobus.*	Field bioassay with *Castanea dentate* seed planted into a mixed deciduous forest. Field EM roots/molecular ID of plants and fungi from root tips.	Dulmer et al. (2014)
Arbutus unedo, *Cistus albidis*, *Quercus ilex*, *Q. coccifera*	151 total OTUs discovered, 3.3 % were found on all four host species, 14 % on three species, 27 % on two species, and 56 % on single hosts; multi-host fungi were the most frequent with 5 of the 8 found on all four hosts	Field EM roots/molecular ID	Taschen et al. (2015)

Arbutoid hosts in other regions also potentially facilitate successional dynamics of neighboring EM hosts. In Eastern Canada, Danielson (1984) synthesized in pure culture several EM fungi associated with *Pinus resinosa* onto *Arctostaphylos uva-ursi*, a common understory prostrate shrub that survives after timber removal. Visser (1995) and Hagerman et al. (2001) concluded that *A. uva-ursi* acts as an important refuge plant following timber harvest and natural disturbance, maintaining fungal diversity and inoculum important to later seral Pinaceae. Similarly, Richard et al. (2005) noted that of 46 rflp EM types found on *Arbutus unedo*, 18 types were shared with *Quercus ilex* in an old-growth Mediterranean forest dominated by *Q. ilex*; they hypothesized that *Arbutus unedo* may play an important role in the early succession dynamics of *Q. ilex*. In a follow-up study, Richard et al. (2009) demonstrated that *A. unedo* facilitated the establishment of *Q. ilex* in a shrub dominated community by enhancing seedling survival and EM colonization, mirroring results of Horton et al. (1999) for Douglas-fir seedling establishment under *Arctostaphylos* in a California chaparral.

More recently, Kennedy et al. (2012) used molecular tools in a field study of the EM fungal community of *Arbutus menziesii* in two sites with intermixed Pinaceae hosts in southwest Oregon. On one site they encountered 126 total fungal taxa on *Arbutus*, 17 of which also occurred with Pinaceae (*Pseudotsuga menziesii* and *Pinus* spp.); in the second site, of 82 total fungal taxa found, 25 colonized *Arbutus* and Douglas-fir, 13 of which were detected on both hosts in single soil cores. They also noted that the EM fungal community associated with *Arbutus menziesii* was phylogenetically similar in structure to that seen with Pinaceae and angiosperms in the genera *Quercus* and *Cercocarpus* in the region. In addition to the numerous "multi-host" fungi supported by *Arbutus*, they also noted that *Arbutus* plants were colonized by two *Rhizopogon* species that are well known Pinaceae specialists, similar to the results reported by Massicotte et al. (1999). Kennedy et al. (2012) describe *Arbutus menziesii* as a "hub" in the CMN in space and time, promoting ecosystem resiliency by maintaining EM fungal diversity, soil microbial processes, and facilitating the establishment of later seral trees. Overall, results from Horton et al. (1999), Richard et al. (2009) and Kennedy et al. (2012) strongly support the earlier hypotheses by Molina and Trappe (1982) and Perry et al. (1989) on the positive feedback provided by these pioneering shrubs and trees in these frequently disturbed plant communities.

1.4.2 Other Examples of Potential Facilitation in Plant Community Dynamics

Similar to arbutoid mycorrhizal plants, pioneering Cistaceae species may facilitate *Pinus* and *Quercus* species establishment in Mediterranean ecosystems (Martin-Pinto et al. 2006), and Quercus in oak savanaahs of the central USA (Dickie et al. 2004). Overlap in EM fungal associates can also shape successional patterns between dominant and subdominant EM forest trees. In Western North America, such facilitation may be involved among *Pinus contorta*, *Picea glauca*, and *Abies lasiocarpa* in British Columbia (Kranabetter et al. 1999), between pioneering lodgepole pine (*Pinus contorta*) and later seral Engelmann spruce (*Picea engelmannii*) in Wyoming, USA, and between Douglas-fir and western hemlock (*Tsuga heterophylla*) in the wet temperate forests of the Pacific Northwest, North America (Smith et al. 1995; Horton et al. 2005). The subdominant tree tanoak (*Lithocarpus densiflora*, Fagaceae), which also occurs as a shrub and stump sprouts following fire, may influence successional dynamics of neighboring Pinaceae, particularly Douglas-fir, through the CMNs of shared EM fungi (Massicotte et al. 1999; Kennedy et al. 2003). The extensive ectomycorrhiza research on the paper birch (*Betula pendula*)—Douglas-fir ecosystem in British Columbia confirmed not only the operlap in shared EM fungi between these EM hosts (Simard et al. 1997a; Jones et al. 1997; Twieg et al. 2007), but also demonstrated the transfer of isotopically labeled carbon from the pioneering birch to the later seral Douglas-fir via commonly shared EM fungi in the field (Simard et al. 1997b).

In one of the larger temperate forest molecular studies of overlap in shared EM fungi between codominant EM tree species, Ishida et al. (2007) examined 8 hosts belonging to 6 genera in three families (Betulaceae, Fagaceae, Pinaceae) in two mixed conifer-broadleaf forests of Japan. Although the EM fungal communities were similar among hosts, a significant portion of fungi showed host specificity, primarily at the family level, but also at the genus level. Some host generalists also showed statistically supported preference towards particular tree species. The authors emphasized that high diversity of EM hosts and the strong display of various host specificities and preferences by the fungi increased diversity among the total EM fungal community, i.e., high EM host diversity in a stand contributes to high EM fungal diversity, a pattern also recently revealed at the global level (Tedersoo et al. 2014). From a successional standpoint, they noted that the higher proportion of broad-host ranging fungi in the secondary forest stand compared to the old growth (primary) forest may benefit *Abies homolepis* (a late successional tree), as it is able to share several mycorrhizal fungi with the early seral broadleaf (angiosperm) species.

Many small stature, understory forest plants associate with diverse EM fungi, and may thus influence EM community dynamics of dominant overstory EM tree species. For example, several species of understory plants in the Pyroleae are widespread in northern temperate forests, survive in dense shade of the forest canopy, and form mycorrhiza with many EM fungi common to overstory EM trees (Tedersoo et al. 2007a; Zimmer et al. 2007; Massicotte et al. 2008; Hynson and Bruns 2009). Although many of the fungi recovered on the roots of Pyroleae in these studies were considered host generalists, Tedersoo et al. (2007a) noted some host preference for *Tricholoma* species and that some pyroloids hosted the Pinaceae specialist *Suillus variegatus*. Similarly, Zimmer et al. (2007) and Hynson and Bruns (2009) noted the Pinaceae specialists *Rhizopogon* spp. in roots of *Pyrola picta*. Such strong overlap between understory myxotrophic Pyroleae and overstory EM hosts for shared EM fungi raises interesting questions regarding the potential ecological interactions between these forest plants.

Potential facilitation via CMNs has also been proposed in tropical forests and the savanaahs of Africa. Alexander et al. (1992) found that seedlings of *Instia palembanica* (Caesalpinaceae) planted in proximity to *Shorea leprosula* (Dipterocarpaceae) more rapidly formed ectomycorrhiza than seedlings planted distant to *Shorea*, and emphasized the practical nature of maintaining *Shorea* trees on harvested forest sites to maintain fungal inoculum for seedlings of *Instia* or other EM hosts. Similarly, Onguene and Kuyper (2002) found survival and ectomycorrhiza formation of *Paraberlinia bifoliota* seedlings planted in contact with four adult EM hosts species were higher for seedlings under *Brachystegia cynometriodes* than under conspecific adults; they noted that this observation may influence a forester’s choice in selecting and maintaining particular tree species after tree harvest. Tedersoo et al. (2011) examined EM fungi on roots of over 30 EM tree host species across 4 sites in wooded savannahs and rainforests of continental Africa and

Madagascar and found that their results support earlier hypotheses that "pioneer Phylanthaceae may facilitate the establishment of late-succession Fabaceae and potentially other EM hosts by providing compatible fungal inoculum in deforested and naturally disturbed ecosystems of tropical Africa." Diédhiou et al. (2010) demonstrated the EM fungus linkage potential between seedling and adult roots of five EM hosts from four genera in a tropical rain forest of Guinea: *Anthonotha*, *Cryptosepalum* and *Paramacrolobium* in Fabaceae, and *Uapaca* in Phyllanthaceae. They concluded that the adult hosts in the EM network "likely function as 'nurse trees' for conspecific and non-conspecific seedlings and therefore promote diversity and coexistence of species in this forest". In neotropical forests, Tedersoo et al. (2010b) and Smith et al. (2011) report similar results for EM fungi associated with diverse EM Fabaceae trees (*Dicymbe corymbosa*, *D. altosonii*, and *Aldina insignis*). They found that the dominance of these Fabaceae EM hosts in this ecosystem, the diversity of EM fungi they support, and the strong overlap in shared EM fungi among the trees may facilitate perpetuation of this EM guild of plants and fungi.

1.4.3 Primary Succession

Pioneering plants in primary succession are well known to facilitate many biological processes, often acting as foci for establishment of later seral plants, and presence of mycorrhizal fungi are key to their establishment (Nara 2008; Nara, Chap.6, this volume). In a series of experiments, Nara and colleagues have demonstrated the facilitative nature of pioneering dwarf willow (*Salix reinii*) on the volcanic desert areas of Mt. Fuji in Japan (Nara and Hogetsu 2004; Nara 2006a, b). Seedlings of *Betula* and *Larix* are commonly observed in close proximity to adult dwarf willow shrubs in this area and were shown to form ectomycorrhizae with several of the same generalist fungi found on willow. Overall, their studies lend strong support to the facilitative nature of pioneering dwarf willow on successional dynamics of later tree establishment as affected by CMNs of mutually compatible fungi. See Nara (Chap. 6, this volume) for more details on this set of elegant experiments.

1.4.4 Potential Exceptions to Facilitation

Although we cite above many potential examples of facilitation as suggested by the frequent ability of diverse host species to share multi-host EM fungi, there are probably widespread exceptions, because EM hosts and fungi can also display various degrees of specificity and preference. Perhaps the best example in this regard is displayed by the EM nature of the genus *Alnus*. As discussed previously, *Alnus* species worldwide associate with a relatively low diversity of EM fungi, many of which are host specialists with *Alnus* (Molina 1981; Tedersoo et al. 2009; Kennedy and Hill 2010; Kennedy et al. Chap. 8, this volume), thus lowering the potential for

CMNs with other nearby EM host species (Horton et al. 2013). In a recent study, Bent et al. (2011) examined shared EM fungal communities and the potential for successional facilitation of *Betula papyrifera*, *Picea glauca*, and *Populus tremuloides* seedlings growing near pioneer *Alnus viridis* shrubs in a recent fire-disturbed boreal ecosystem in interior Alaska. They found that the *A. viridis* EM fungal community contained several *Alnus* specialist fungi, and was distinct from the fungal communities noted on the adjacent three hosts. Although there was minimal overlap between alder and the other three hosts via minor ribotypes, the *Populus* and *Betula* seedlings showed a strong overlap in shared fungi and a moderate overlap with *Picea* seedlings. They concluded that a facilitative relationship between *Alnus* and the other three hosts was unlikely, but that the *Populus*, *Betula*, and *Picea* hosts had high potential for interacting with each other through CMNs. For more on *Alnus* mycorrhizal networks see Chap. 8 in this volume by Kennedy and colleagues.

Some distantly related EM host genera might display little overlap in compatible EM fungi when growing in proximity, limiting potential facilitation. For example, Smith et al. (2009) found different EM fungal community structure and strong host preference in a stand of mixed *Quercus* and *Pinus*; with the exception of a few "multi-host" fungal taxa, most of the dominant EM fungi on *Pinus* rarely associated with—or had low frequency on *Quercus*, and vice versa. They concluded that "multi-host" fungi may be less dominant in some EM systems than previously thought. However, high host preference in an EM system does not necessarily rule out abundant overlap in shared EM fungi and potential facilitation effects. For example, Morris et al. (2008) found contrasting EM fungal communities on two co-occurring oaks in California. However, 40 of the 140 fungal taxa identified occurred on both hosts, and 13 of the 16 most frequent fungi were shared between the two oaks. When Morris et al. (2009) examined two neighboring oak species in a tropical cloud forest in southern Mexico, of 154 EM species recovered, 62 (40 %) occurred only on *Quercus laurina*, 52 (34 %) only on *Q. crassifolia*, yet 40 (26 %) occurred on both. Similarly, Aponte et al. (2010) noted significant host preference among EM fungi for neighboring *Q. canariensis* and *Q. suber* in southern Spain, yet they still shared about 20 % of the total EM fungi recovered. Tedersoo et al. (2008a) also showed strong host preference in a Tasmanian wet sclerophyll forest among *Eucalyptus regnans*, *Ponaderrisa petala*, and *Nothofagus cunninghamii*; "two thirds of the most common EM fungi from several linages was significantly influenced by host species." Still, they note that the ability of *Nothofagus cunninghamii* and *Eucalyptus* to associate with the same EM fungi may facilitate late-successional *N. cunninghamii*.

1.4.5 Potential for Long-Term EM Legacies to Affect Plant Migration During Climate Change

EM hosts migrated during past episodes of climate change and will continue to do so under current climate change scenarios (Jacobson et al. 1987). The ability for EM fungal species to colonize diverse EM hosts will affect EM host migration

(Perry et al. 1990; Molina et al. 1992). The EM condition of *Dryas octopetala* in Ireland provides an interesting example of past and potential future legacy. Although primarily a widespread arctic and alpine shrub, *D. octopetala* occurs as a relict population in the lowland grassland-heath in northern Ireland (called the Burren); this area harbored *Pinus sylvestris* forests about 1500 years ago. Harrington (2003) and Harrington and Mitchel (2002, 2005a, b) conducted extensive studies of the EM fungi (sporocarps and EM root tip surveys) and found high diversity of EM fungi. Many of the species found fruiting and on roots are well known EM associates of European woodland forest trees and exhibit a broad host range (Harrington and Mitchell 2002). They hypothesized that *D. octopetala* has maintained the EM fungal community it shared in common with *Pinus* when the two hosts cohabitated the sites. Thus, if EM host trees migrate northward into this region as climate warms, the relict EM fungal community maintained by the *Dryas* legacy would be present to facilitate tree establishment. A similar case can be made for *Dryas* and other EM shrub hosts in Arctic and alpine communities. Ryberg et al. (2009) describe a rich EM fungal community on *D. octopetala* and *Salix reticulata* in an alpine cliff ecosystem; they identified about 70 potential EM fungi and noted low host specificity or preference between *Dryas* and *Salix*. They concluded that the hosts seem likely to facilitate succession of the alpine tundra to subalpine forest by serving as mycorrhizal partners for establishing pioneer trees. The rich EM fungal community on *Dryas* and *Salix* in alpine and arctic locations in Norway (Frederikke et al. 2010), Sweden (Ryberg et al. 2011) and North American (Fujimura and Egger 2012; Timling and Taylor 2012) may do likewise. Timling and Taylor (2012) note that 73 % of the EM fungal ITS OTUs they found on EM root tips of *Dryas integrifolia* and *Salix arctica* in Arctic habitats occur in regions outside the Arctic. These communities are ripe for manipulative experiments to test the hypothesis that ectomycorrhizal fungi associated with *Dryas* and *Salix* will facilitate establishment of migrating EM hosts during climate change.

Krpata et al. (2007) demonstrate similar potential for *Arctostaphylos uva-ursi* to act as legacy plants for afforestation of subalpine and alpine habitats. They observed a diverse group of fungi associated with *A. uva-ursi* based on sporocarp collections, mycorrhiza morphotypes and molecular identification from root tips. Although they considered the majority of EM fungi “generalists”, they also discovered that several EM fungi considered specific to other EM hosts developed arbutoid mycorrhizae, e.g., *Lactarius deterrimus* (host specific to *Picea*), *Suillus plorens* and *S. grevillei* (host specific to *Larix*). Mühlmann and Göbl (2006) also discovered *L. deterrimus* forming arbutoid mycorrhizae with *A. uva-ursi* in the Swiss Alps. As noted above for arbutoid host legacies, Krpata et al. (2007) conclude that the ability of *A. uva-ursi* to maintain a high diversity of generalist and specialist EM fungi in these ecosystems, even though they have been treeless for 400 years, may facilitate future afforestation or natural migration of EM tree hosts.

1.4.6 Evolutionary Processes in Specificity Phenomena

This is an exciting time to be doing research on mycorrhizal symbioses with genomic approaches providing important new insights into the evolution of the symbioses and a better understanding of mycorrhiza ecology, including specificity phenomena. To date the genome of one species in Glomeromycota has been sequenced while over 25 ectomycorrhizal fungi have been sequenced from both Basidiomycota and Ascomycota. Glomeromycota are an ancient lineage (Berbee and Taylor 1993; Redecker et al. 2000; Remy et al. 1994) whose appearance in the fossil record over 400 million years before present coincides with the first land plants. Although thought to be entirely clonal, there is evidence for recombination in the group (Croll et al. 2008)) and meiosis specific proteins have now been found (Tisserant et al. 2012). To date, there are close to 250 Glomeromycota species identified by spore morphology, but analyses of environmental ribosomal sequences suggests the richness is closer to 350 or even 1600 operational taxonomic units (Kõljalg et al. 2013; Öpik et al. 2013; Schüssler 2015). Our ability to clarify the diversity of this enigmatic group is hampered because they are not free living, they are ceonocytic with few or no septa separating the nuclei into discrete cells, most have not been cultured (e.g., with bait plants or transformed carrot roots; Ohsowski et al. 2014) and individuals contain multiple genotypes making sequencing problematic. These same issues make our ability to analyze specificity phenomena difficult given the difficulty in identifying fungal species and even individuals in Glomeromycota.

While the Glomeromycota appear to have evolved the mycorrhizal habit only once (van der Heijden et al. 2015), ectomycorrhizal fungi may have independently evolved the symbiotic habit more than 78 times (Tedersoo and Smith 2013). The first ectomycorrhizal fungal species evolved from litter decay fungi about 200 million years ago with little evidence for any species evolving from pathogenic fungi (James et al. 2006; Plett and Martin 2011). Although ectomycorrhizal fungi evolved from saprotrophic lineages and maintain varying levels of saprotrophic capabilities (i.e., can grow on agar), they lack many genes involved in litter decomposition and to date, none are known to be free living in nature (Martin et al. 2008, 2010; van der Heijden et al. 2015).

Genomic evidence from all three phyla of mycorrhizal fungi (Glomeromycota, Ascomycota, and Basidiomycota) indicates that mycorrhizal fungi disrupt the host defense system. However, the molecular tools evolved independently with unique pathways as one may expect given their unique evolutionary histories. For instance, Laccaria bicolor produces a small secreted protein (MiSSP7) that disrupts the plant's jasmonic acid signaling pathway and suppresses the host defense system (Plett et al. 2014). Another small secreted protein, SP7, is produced by the AM fungus *Rhizophagus irregularis* (formally *Glomus intraradices*) and also disrupts the host immune response (Kloppholz et al. 2011). The general pattern may hold for other species as well, and with different proteins and through interactions with different parts of the host defense system. Specificity phenomena are likely governed by similar host-fungus genetic cross talk, but much work is needed on the genetics of specificity interactions. The number of complete ectomycorrhizal fungus genomes available is now at 27 species (van der Heijden et al. 2015) and many more are on the way (Grigoriev et al. 2014). Similar advances are on the way in Glomeromycota, but this group is proving difficult because of its unique genetic system. With these genomic data, our understanding of the evolution of mycorrhiza specificity will rapidly improve.

1.5 Summary and Conclusions

The review of host specificity phenomena by Molina et al. (1992) was shaped largely by evidence from fruitbody occurrence in field settings and direct observations of compatibility based on bioassays and pure culture synthesis experiments. Although these same approaches remain useful for understanding mycorrhiza specificity, the revolution in molecular approaches over the last 20 years has enhanced our ability to examine mycorrhiza specificity at the root tip scale in both greenhouse and field settings (Gardes and Bruns 1993; Bruns et al. 1998; Horton and Bruns 2001). Genome sequences and modern phylogenetic analyses provide considerable new data to examine evolutionary patterns of mycorrhizal symbioses (Kohler et al. 2015; Plett and Martin 2011) with implications for understanding specificity relationships between diverse taxa of plants and fungi. Most importantly, molecular technology has spread to labs around the world, providing data and enhancing our understanding of EM fungi from diverse ecosystems and plant communities.

The following points summarize our general conclusions.

1. Given the complexity of specificity patterns discussed and the dependency of results on the context of the study, we urge caution in overgeneralizing on global patterns of specificity phenomena among diverse fungal and plant taxa.
2. Mycorrhizal networks are directly impacted by specificity phenomena. Evidence strongly suggests that CMNs play a role in plant community dynamics but additional field-based empirical evidence for this role is needed. This knowledge provides tools for resource managers to maintain resilient ecosystems in the face of growing resource extraction and climate change (e.g., maintaining legacy host plants, plant diversity, and avoiding oversimplification of ecosystems).
3. Varying degrees of specificity occur at all levels in the taxonomic hierarchy, although specificity at the species level appears rare. It is important for authors to clearly define terms when discussing host specificity. For instance, we suggest labeling an EM fungus a *Quercus* specialist or Fagaceae specialist depending on the phylogenetic breadth of known hosts.
4. Virtually all ecological communities are dominated by a few species with many others being rare, and ectomycorrhizal fungus communities are no different. Most species that are frequently sampled tend to be found on multiple hosts. In contrast, rarely or infrequently sampled species tend not to be found on multiple

hosts. Therefore, the number samples included in a study impacts the view of host preference and even specificity. Increased sampling efforts and statistical tools for assessing specificity phenomena in the field are enhancing our ability to assess host specificity and preference patterns (Hoeksema, Chap. 9, this Volume).

5. Global understanding of specificity phenomena requires sampling of fungi in multiple communities and in multiple ecological settings—most fungal species remain undersampled.
6. Genomic studies are providing and will continue to provide insights into specificity phenomena.

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