
Investigating the disparity in host specificity between AM and EM fungi: lessons from theory and better-studied systems

Jason D. Hoeksema, Graduate Group in Ecology, Section of Evolution and Ecology, Univ. of California, Davis, CA 95616, USA (jdhoeksema@ucdavis.edu).

Over 80% of vascular plant species are associated with some type of mycorrhizal fungus (Trappe 1987). These associations are thought to be mutualistic in many cases, with the host plant exchanging photosynthate with the fungus in return for mineral nutrients (Harley and Smith 1983, Smith and Read 1997). The two most abundant and studied mycorrhizal types are ectomycorrhizal (EM) fungi and arbuscular mycorrhizal (AM) fungi. A generally agreed-upon phenomenon is that AM fungi are broad generalists with respect to the number of host plant species with which they can associate (Smith and Read 1997). Because of the difficulty of detecting variation in the relative abundances of AM fungal species on plant roots, as well as the difficulty of understanding the causes (environmental factors, host genotype, interspecific interactions) of such variation, there exist gaps in our knowledge about the extent to which AM fungal species associate with different plant species, especially in complex natural fungal communities. However, based on evidence accumulated so far from field and laboratory observations, AM fungi exhibit broad host ranges, and the rare exceptions to this (e.g., Graw et al. 1979) "must not be allowed to cloud the observation that VA mycorrhizal fungi and their host plants have generally non-specific interactions" (Smith and Read 1997). In contrast, specificity among EM fungi ranges from very broad to extremely specific, with many EM fungi associating with only a single host plant species (Janos 1980a, Alexander 1989, Harley 1989, Borowicz and Juliano 1991, Molina et al. 1992, Smith and Read 1997). Explanations for the disparity in host specificity between the two types of fungi have been mentioned briefly in other contexts, but have not been developed, tested, or compared with other potential explanations (e.g., Janos 1980b, 1983, Malloch et al. 1980, Connell and Lowman 1989, Molina et al. 1992). There is clearly a need to explicitly develop and test a set of hypotheses explain-

ing the higher incidence of host-specificity among EM fungi than among AM fungi.

The general topic of specificity is one of broad interest to ecologists and evolutionary biologists, as the degree of specificity in interactions is predicted to strongly influence the nature of evolution of those interactions (e.g., whether two species co-evolve) (Janzen 1980, Thompson 1994). As a result, it has received a great deal of attention both theoretically and empirically. Much of this work has focused on specificity in interactions between plants and their herbivores (e.g., Futuyma and Moreno 1988, Berenbaum 1996), pollinators (e.g., Kiestler et al. 1984, Waser et al. 1996), and fruit dispersers (e.g., Jordano 1987, Fleming et al. 1993). The voluminous literature generated from investigations of these three types of interactions provides valuable information and predictions about specificity phenomena. Many of these predictions are particular to specific systems, but some are very general and could aid in attempts to understand specificity in mycorrhizal mutualisms. However, these results have not been utilized to help understand the disparity in host specificity between AM and EM fungi. Here I discuss three principles regarding the evolution of specificity that emerge from an examination of the plant-herbivore, plant-pollinator, and plant-fruit-disperser literature and other theoretical literature. These three principles suggest three hypotheses (not mutually exclusive) for the disparity in host specificity between AM and EM fungi, which I discuss and evaluate.

Principle # 1. Lack of variation in the benefits of association among potential partners in an interaction discourages the evolution of specificity on any of those potential partners.

A limited amount of theoretical work has addressed variation in benefits among potential partners in mutu-

alisms, and the effect of this variation on specificity (Fleming et al. 1993, Waser et al. 1996). For example, Waser et al. (1996) present a simple mathematical model that predicts that plants will be generalists with respect to pollinators if different pollinators are similar in their effectiveness. Similarly, they predict pollinators will generalize with respect to plant species if rewards are similar across plant species. The idea behind this model is that if potential partners are similar in the benefits they would confer on a mutualism, there will be no selection for specialization on any subset of those potential partners (Feinsinger 1983). This idea has not been thoroughly tested for any taxon, but a number of investigators have measured the variation in effectiveness of plant pollinators or seed dispersers with the intent of testing the hypothesis that similarity was limiting specialization in that system (Schemske and Horvitz 1984, Fishbein and Venable 1996, Larson 1996). For example, Schemske and Horvitz (1984) demonstrate variation in pollination effectiveness among pollinators of a neotropical herb, and suggest that such demonstrations are crucial for understanding the evolution of specificity in mutualisms.

This principle suggests one hypothesis to explain why AM fungi are less specialized on their hosts than EM fungi: *that variation in benefits to AM fungi among host plants is smaller than that among the host plants of EM fungi, and this lack of variation has limited host-specialization in AM fungi relative to EM fungi (Hypothesis # 1)*. Despite the potential difficulty of measuring benefits of plants to mycorrhizal fungi, this hypothesis is potentially very useful in understanding specificity in mycorrhizal relationships. Finding significant differences in benefits to AM fungi among AM plant hosts would suggest rejection of this hypothesis. Finding negligible differences in benefits to EM fungi among all potential EM plant hosts would also be grounds for rejecting this hypothesis.

In fact, benefits to mycorrhizal fungi of the association with plant hosts have not often been measured. Usually, only the benefit to the plant is quantified, as is the case in most studies of reputedly mutualistic interactions with plants (Bronstein 1994). No mycorrhizal fungi have been found to successfully reproduce apart from plant hosts (Molina et al. 1992), and thus the benefit to them of the association could be considered to be always qualitatively positive. However, more studies are needed that compare quantitative measures of fungal success (such as the number of spores produced, or total hyphal biomass) among a variety of potential plant hosts. In the few cases when these data have been collected for AM fungi, enough variation among plant species in benefits to the fungi seems to exist to allow for at least the potential evolution of specificity in AM fungi. Bever et al. (1996) found differential sporulation of AM fungi among different plant host species, and suggest that this and other

recent studies (e.g., Johnson et al. 1991, Sanders and Fitter 1992, Hendrix et al. 1995) indicate significant dependence of AM fungal performance on the plant host species involved. Though Hypothesis # 1 has not been sufficiently tested for most fungal taxa, this information suggests that additional hypotheses are necessary to explain the lack of host specificity in AM fungi in particular, and the disparity in host specificity between AM and EM fungi in general.

Principle # 2. Clades may contain a high proportion of host specific species because the ancestors were host specific, i.e., the lineage is "committed" by its physiology or morphology to host specificity.

Futuyma and Moreno (1988) suggest that these mechanisms may explain macroevolutionary patterns of specialization and generalization in some cases. They discuss examples of lepidopterans and their host plants in which evolutionary constraint (or "phylogenetic inertia") seems to have resulted in many specialist species on similar resources. Law and Koptur (1986) present a simple mathematical model that predicts mutualistic specificity is more likely to evolve further if some degree of specificity in an interaction already exists. As an example, they suggest that in the hermit and non-hermit hummingbirds, specificity has led directly to further specificity in the evolution of those taxa (Stiles 1975, Feinsinger 1983).

Principle 2 suggests the hypothesis that *when host specificity is present in EM fungal taxa, it is present simply due to its presence in a common EM fungal ancestor, coupled with a low probability of reversion from a specialized to a generalized strategy (Hypothesis # 2)*. According to this hypothesis, specificity in the EM fungi need only to have evolved once to account for its prevalence in the EM fungi today. Futuyma and Moreno (1988) discuss how this type of hypothesis might be tested. If the specialized taxa in a lineage are all specialized on the same resource, we can infer that selection has not necessarily been for specialization in all of those taxa, but that many of them might be specialized simply because their most recent ancestor was specialized. Alternatively, we might find that in a lineage containing many specialists, the specialists are specialized on a variety of resources. To the extent that this is true, we might infer that selection has been for specialization per se, and that Hypothesis # 2 should be rejected. Menken (1996) performs such an analysis of moth species in the genus *Yponomeuta* and their specialization as herbivores on plants primarily in the family Celastraceae. By mapping host-plant associations as characters onto an independently derived estimate of the insect phylogeny, Menken (1996) generates hypotheses about the evolution of *Yponomeuta* and its hosts, concluding that *Yponomeuta* species are probably committed to specialization per se rather than to particular plant groups.

In fact, the EM fungi (in contrast to the monophyletic AM fungi) are far from being a monophyletic group, and narrow host range of EM fungi (association with only one host genus) has evolved in at least twenty different fungal families and two major fungal divisions (Basidiomycotina and Ascomycotina) (Molina et al. 1992). Many of these families contain just as many species of fungi with intermediate or broad host ranges. Furthermore, the host plant genera on which the fungi specialize vary a great deal within most of the fungal families containing host-specific fungi. Thus, Hypothesis #2 probably does not account for most of the specificity found in the EM fungi. However, a formal phylogenetic analysis (e.g., as in Menken 1996 or Muller 1996) of the EM fungi and their host associations would better reveal the proportion of specificity accounted for by ancestral specificity.

Principle # 3. Sufficient temporal or spatial variation or unpredictability in the abundance or quality of potential partners in an interaction will, over evolutionary time, prevent specialization on any of those potential partners. In other words, selection will act against those taxa that specialize on inconsistent or unpredictable taxa.

Futuyma and Moreno (1988) review hypotheses about the evolution of specialization and generalization, and suggest that in most general models, the evolution of specialization tends to be favored by environmental constancy. In fact, a preponderance of researchers on the evolution of specialization have suggested that the evolution of specialization on a host or resource is unlikely unless that host or resource is relatively predictable and consistent (Dethier 1954, Levins 1962, 1968, Levins and MacArthur 1969, Schoener 1971, Gillespie 1977, Keeler 1981, Boucher et al. 1982, Thompson 1982, Howe 1984, Lacy 1984, Schemske and Horvitz 1984, Law 1985, Herrera 1988, Peterson 1995, Fry 1996, Waser et al. 1996). Waser et al. (1996), for example, introduce a simple mathematical model that predicts both that plants will be generalists with respect to pollinators if temporal and spatial variance in pollinator quality is appreciable, and that pollinators will be generalists with respect to plants if pollinator lifespans are long relative to flowering duration of individual plant species. Also, they predict plants may specialize on one or a few pollinators if the pollinator populations fluctuate little (Waser et al. 1996).

Some data from plant-herbivore, plant-pollinator, and plant-seed-disperser systems seem to support Principle # 3. Otte and Joern (1977), Cates (1980, 1981), and Lawton and Strong (1981) found greater prevalence of polyphagous insect species on annual plants, and more monophagous species on herbaceous and woody perennials. Coupled with the assertion (Levin 1984, Niklas et al. 1985) that populations of short-lived

plants are often semi-isolated, occupy transient habitats, and experience unpredictable fluctuations, this implies greater specialization on less ephemeral resources. Malloch et al. (1980) cite studies of tropical parasitoid insects (Janzen 1976) and bark beetles (Beaver 1979) and suggest that in these taxa, the hosts may simply be too rare to allow extreme specialization. Fox and Morrow (1981) present data supporting the idea that herbivores will be generalists over time if host plant availability is shorter than the insect generation time. Jordano (1987) reviews mutualisms and finds a similar pattern with bees as pollinators and for tropical frugivorous birds as seed-dispersers. Lacy (1984) reports a negative association between mean host duration and measures of the diversity of host species used by 10 species of mycophagous Drosophilidae. In other words, Drosophilidae species exploiting the most ephemeral fungal resources tend to be generalist feeders. These empirical studies all support the idea that selection acts against taxa that specialize on rare, inconsistent or unpredictable hosts.

Altogether, this body of theoretical and empirical work strongly suggests a third hypothesis to explain the higher incidence of host specificity in EM fungi versus AM fungi: *that some of the plant hosts of EM fungi are relatively constant in abundance over space and time which allows specialization, and the plant hosts of AM fungi are less constant over space or time, preventing specialization (Hypothesis # 3).* If AM fungi tend to associate with plants that are unpredictable in time or space, for example annuals or locally rare plants as opposed to perennial and locally abundant plants, then selection may have acted against attempts to establish host-specific relationships over evolutionary time.

A test of this hypothesis would consist of quantifying the host-specificity of mycorrhizal fungus species in a given system, as well as the constancy over space and time of potential host plants. If host-specificity of the fungi was found to vary independently of plant host spatial and temporal constancy, we would reject this hypothesis. Specifically, if within potential plant hosts of EM fungi the more temporally and spatially constant plant species harbor more host-specific EM fungi than do the less constant host plants, and if within-plant hosts of AM fungi we found that more constant hosts (over space and time) foster a higher degree of host specificity, we could not reject this hypothesis.

Some circumstantial evidence exists that addresses Hypothesis # 3. EM fungi are primarily associated with perennial, woody plants that dominate some forest communities in both tropical and temperate regions (Malloch et al. 1980, Alexander 1989, Allen et al. 1995, Smith and Read 1997). For example, in temperate North America, Douglas fir (*Pseudotsuga menziesii*) is a persistently dominant member of forest communities over a broad geographic range. Douglas fir also hosts one of the largest known assemblages of genus-specific

EM fungi (ca 250 spp.) (Molina et al. 1992). Similarly, members of a few plant families (e.g., Caesalpinaceae, Dipterocarpaceae) often form relatively mono-dominant forests in many tropical regions (Connell and Lowman 1989, Hart et al. 1989). These forests are also ectomycorrhizal, and harbor some of the most host-specific EM fungi described (Molina et al. 1992, Smits 1992). In contrast, AM fungi in temperate regions typically (but not always) associate with herbaceous plants (which can be considered relatively inconstant over time relative to large, woody species). In the tropics and in some temperate areas, AM fungi are associated with long-lived woody plants, but these forests are usually highly diverse with individuals of tropical forest species being widely separated from the nearest conspecifics (Fedorov 1966, Malloch et al. 1980; but see Torti et al. 1997). Thus the woody plant hosts of AM fungi, despite being potentially predictable over time, are often effectively unpredictable and inconstant over space relative to the woody plant hosts of EM fungi. These observations are all consistent with the third hypothesis outlined above: that, over evolutionary time, the association of AM fungi with temporally and spatially unpredictable plant species may have discouraged the evolution of highly host-specific AM fungal species. Furthermore, enough constancy over space and time seems to exist in some of the typical hosts of EM fungi to have allowed for the evolution of host specialization by EM fungi.

As discussed above, we do not have complete information on the host specificity of mycorrhizal fungi, especially of AM fungi. Hypothesis # 3 predicts that if host-specific AM fungi are found, it will be in a near mono-dominant forest composed of AM fungal host plants, a situation that until recently (Torti et al. 1997) had not been reported. Similarly, AM host specificity might be found in the tallgrass prairie of the midwestern United States, in which an AM fungal host plant, big bluestem (*Andropogon gerardii*), is a dominant, long-lived, and fairly temporally and spatially predictable member of the plant community. These traits might at least allow for the possibility of specialization on big bluestem by AM fungal taxa. However, Hypothesis # 1 suggests that even in situations where host plant predictability is sufficient to allow the possibility of specialization by a fungus on a particular host plant, there still may not be selection for specialization if benefits to the fungus in question do not differ sufficiently among potential host plants.

The modes of dispersal of AM and EM fungi may serve to exaggerate differences between them in host plant constancy or predictability over space. EM fungi are generally considered to be better dispersers than AM fungi, since most EM fungi produce fruiting bodies which are either aboveground (allowing effective spore dispersal by wind) or are dispersed by rodents (Molina et al. 1992, Smith and Read 1997). AM fungi, on the

other hand, do not produce fruiting bodies, but produce spores belowground which do not attract mammalian dispersers and thus are moved by animals only short distances or incidentally. Thus, a host plant species whose individuals are widely spaced would be experienced by poorly-dispersing AM fungi as being relatively unpredictable over space, while that same plant would be more predictable over space for an effectively dispersing EM fungus. Law (1985) discusses this idea, but does not believe that EM fungi are any more host specific than AM fungi, and consequently sees no need to explain the higher incidence of host specificity in EM fungi.

Interestingly, most authors discussing mycorrhizal host specificity in relation to host dominance in forests (e.g. Baylis 1975, Janos 1980b, 1983, Connell and Lowman 1989, Allen et al. 1995, Smith and Read 1997) have not developed the possibility that host plant dominance may have allowed the evolution of host specificity by some EM fungi and that host plant unpredictability over space or time may have limited the evolution of host specificity in AM fungi (Hypothesis # 3). Instead, they have focused on the possibility that the specificity of some EM fungi for their hosts might contribute to their host's ability to dominate a forest (see Connell and Lowman 1989 for the most thorough development of that hypothesis). I suggest that more attention should be paid to the possibility that EM host plant mono-dominance may have allowed EM fungi to specialize on those host plants, and that AM host plant unpredictability has prevented the evolution of host specialization by AM fungi.

Conclusions

Principle # 3, the idea that constancy in abundance or quality of a partner over space and time is necessary for the evolution of specialization on that partner, is a prevalent idea in models of the evolution of host specificity and seems to provide the most insight into the disparity between EM and AM fungi in degree of host-specificity. While more data need to be collected and analyzed according to the recommendations outlined above (including data to more thoroughly test Hypothesis # 1 and Hypothesis # 2) in order to understand the processes leading to specialization in the EM fungi, the lack of constancy over space or time in the plant hosts of most AM fungi may be sufficient to explain the lack of host specificity found in that group (Hypothesis # 3). Other authors (Malloch et al. 1980, Janos 1983, Connell and Lowman 1989, Molina et al. 1992) have hinted either that host constancy of EM fungi might have allowed specificity, or that host inconstancy may limit AM fungal specificity. However, this essay represents an attempt to explicitly outline multi-

ple hypotheses for the disparity in host specificity between EM and AM fungi, drawing on the extensive work of others on the topic of host specificity, and to suggest how these hypotheses should be tested.

Hypothesis #3 suggests that the host-specificity of AM and EM fungi is influenced by the characteristics (spatial and temporal predictability) of their typical host plants. If this is true, then the next logical question to ask is, "Why are EM and AM fungi associated with those typical host plants in the first place?" The answer to this question, which has begun to be addressed (e.g., Harley 1989, Trappe 1989, Allen et al. 1995), would then represent the true independent variable influencing host specificity in EM and AM fungi.

Acknowledgements – A. Amezcua, J. Bergelson, G. M. Mueller and J. A. Rudgers provided helpful comments on earlier drafts of the manuscript. The ideas in this essay benefited from discussions with other participants in the 2nd International Conference on Mycorrhizae in Uppsala, Sweden, July 1998. This material is based upon work supported under a National Science Foundation Graduate Fellowship.

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