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REVIEW PAPER

General principles in the community ecology of ectomycorrhizal fungi

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Abstract

- ***Introduction*** Knowledge of the factors that determine ectomycorrhizal fungal community structure is essential in many areas of practical significance including conservation, habitat restoration, prevention or amelioration of species invasions, and the prediction of responses to climate change. With respect to these goals, however, community ecology, in general, and ectomycorrhizal fungal community ecology, in particular, have been rather disappointing.
- ***Discussion*** Indeed, some feel that community ecology is, at best, an esoteric discipline and, at worst, an inane one. But there is hope. As we apply what has been learned about other organisms concerning the relationships between functional traits and success (abundance), it may be possible to elucidate general principles that govern much of the structuring of ectomycorrhizal fungal communities.
- ***Conclusion*** A hierarchical model of ectomycorrhizal fungal community structure is presented that involves abiotic filtering of immigrant propagules based on functional traits, followed by interspecific competition as ameliorated by disturbance and habitat partitioning, the outcomes of which are dependent on functional traits.

Keywords Community structure · Ectomycorrhizal fungi · Trait · Environment · Hierarchical model

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1 Introduction

Community ecology is the study of species that co-occur in time and space. The particular species present and their relative abundances determine what is frequently referred to as "community structure". The importance of studying communities, as opposed to individual species, stems from the fact that it is the interactions among species that determine many important ecosystem functions including nutrient cycling, carbon storage and productivity. While in this contribution, emphasis is definitely placed on communities of ectomycorrhizal fungi, reference will be made occasionally to other kinds of communities when they illustrate more clearly an important concept.

There has been some recent debate as to the success of community ecologists. While some have suggested that community ecology amounts to a failed effort, others feel that there is hope, particularly if we employ a trait-based approach capable of producing general rules governing community assembly (see McGill et al. 2006 for a short discussion of this topic). Whether we achieve success as community ecologists, however, depends on our goal as much as our approach. After all, if one has no goal, one cannot fail to achieve it. A goal of many community ecologists has been to understand the determinants of the structure of a community. With respect to this goal, we do not feel we have been complete failures. Indeed, we have discovered many of the important factors that govern community structure from studies of specific communities. For example, we now know that the structure of ectomycorrhizal fungal communities is affected by various ecological factors and management practices including soil type (Gehring et al. 1998), fire (Grogan et al. 2000; Chen and Cairney 2002; Anderson et al. 2007), herbivory (Gehring and Bennett 2009), canopy gap formation (Grebenc et al. 2009), soil fertility (Kranabetter et al. 2009), liming (Kjøller and Clemmensen 2009; Rineau et al. 2010), heavy metal pollution (Markkola et al. 2002), land use history (Diedhiou et al. 2010) and urbanization (Baxter et al. 1999). It stands to reason that the structure of a community is altered by such factors and practices because the component species respond in different ways to them.

On the other hand, if the goal is to *predict* the structure of a particular community, meaning its resident species and their relative abundances, perhaps, then, the record of accomplishment is not as stellar. So far, predictions of this sort have simply not been possible. Perhaps, this is why some have called community ecology "repugnant and intractably complex" (Pianka 1992) or, simply, "a mess" (Lawton 1999). More hopeful individuals have suggested that, by accumulating a sufficiently inclusive, worldwide dataset of traits of species, one could eventually predict community structure (Grime 2006; McGill et al. 2006). Thus far, however, we do not appear to be particularly close to reaching that goal. Indeed, it seems rather unlikely that we will ever be able to catalog enough of the relevant traits of enough species to ever make community ecology a predictive science. For one thing, how many traits would be necessary? One recalls with wonder, amazement and some degree of revulsion the *n*-dimensions of Hutchinson's "hypervolume" (Hutchinson 1957). Moreover, because competitive outcomes may depend on various environmental conditions (Erland and Finlay 1992; Mahmood 2003), unless one can accurately predict future environmental conditions or declare competition to be utterly unimportant in structuring communities (Grime 2006), it seems unlikely that community structure can be predicted from a database of species traits.

Perhaps, we are simply unambitious, but, unlike McGill et al. (2006), we find it quite satisfying to know that community ecology actually has produced general principles, even if it has not produced general rules (Lawton 1999). General rules such as "the community is expected to lose species with trait A and gain species with trait B if minimum winter temperatures increase from X to Y" may not yet be attainable. But, the idea that temperature influences community structure is a valuable general principle, even if it does not yield specific predictions in all communities. The goal of this contribution, therefore, is not to produce general rules, or even to advocate that we produce them, but to highlight an approach that is likely to reveal general principles.

2 Defining the community

One of the most basic challenges we face in studying biological communities concerns how we define them in the first place. One can easily appreciate that the definition of "community" will determine how much of it we understand. Parker (2004) has highlighted some of the variation in the definition of community. In some cases, a community comprises all organisms that live together in the same place at the same time. This seems to be the most obvious and natural way to define a community. After all, when we describe human communities, we normally include men, women and children, butchers, bakers and candlestick makers, and everyone else who lives in the same place, irrespective of ethnicity, religion or political persuasion. We may even include all the cats and dogs and other household pets. Each member of such a community interacts with the others in some fashion by virtue of his or her contemporaneity and physical proximity. Studies of biological communities at this level include those concerned with the multiple trophic levels of food webs, and food web approaches are necessary in the study of important ecosystem processes such as energy flow and carbon and nutrient cycling.

In other cases, one might consider a community with a more limited membership. For example, one might have reason to focus on a particular subset of a human community such as members of a single ethnicity. The fungi in the phylum Basidiomycota comprise such a subset of organisms in forest communities. Clearly, Basidiomycotan fungi interact with other species in the forest including fungi in other phyla (Wu et al. 2005), animals from which they obtain nitrogen (Klironomos and Hart 2001), bacteria that can be stimulated or suppressed by them (Olsson and Wallander 1998), and plants that serve as sources of reduced carbon. Despite frequent and ecologically important interactions with such disparate species, the concept of a Basidiomycotan community is still meaningful. Because all Basidiomycotans share a common phylogeny, the organization of the community reveals patterns of adaptive radiation and niche differentiation.

Another subset of human communities might comprise individuals of a given profession. For example, one might speak of the "legal community" including lawyers and judges. Many modern studies in community ecology concern similarly restricted communities, those of a guild of trophically similar species. Hubbell's "Unified Neutral Theory" (Hubbell 2001), for example, restricts itself to within-trophic-level diversity. Thus, according to this view, saprotrophic and biotrophic Basidiomycotans are treated as members of separate communities, which is the approach taken by most ectomycorrhizal fungal ecologists. This within-trophic-level approach to communities seems to be rather traditional; many of community ecology's roots lie in the myriad studies of plant communities comprising trophically similar (photosynthetic) higher plants. In communities of a single trophic level, component species will require common resources. Competition and factors that modify competition, therefore, are likely to be important in structuring them (Fleming 1985).

In addition to these very different views about what constitutes membership in a "community", community ecology is further complicated by the multiplicity of spatial scales at which communities are studied. For example, communities of ectomycorrhizal fungi might be distinguished at the scale of continents (Barroetavena et al. 2007; Claridge 2002), at the scale of vegetation types within a continent (Molina et al. 1992), or within vegetation types (Harrington and Mitchell 2005). Ectomycorrhizal fungal communities may comprise a small stand of trees (Koide et al. 2005a; Ishida et al. 2007), a single tree (Cowden and Peterson 2009), or even a portion of a single root system (Deacon et al. 1983)! How can we begin to make progress in community ecology if we first cannot define its members?

In the conceptual model developed herein, we consider interspecific competitive interactions to be potentially important in structuring communities of ectomycorrhizal fungi. For example, competition may occur among ectomycorrhizal fungi for roots as a carbon source. While many ectomycorrhizal fungi exhibit saprotrophic capabilities, it seems safe for now to assume that, for at least a portion of their life cycles, all ectomycorrhizal fungi are biotrophic (Koide et al. 2008). If competition for roots dominated the assembly of communities, the model presented herein would apply most appropriately to ectomycorrhizal fungal species colonizing a single host species. But, competition may also occur among ectomycorrhizal fungi for common resources found in the soil, including water, nitrogen, phosphorus, etc. If competition for any of those resources were important in the assembly of communities, then we probably ought to consider the community to comprise species that could potentially interact in the soil, irrespective of host species.

Thus, whether a "host filter" (see Jumpponen and Egerton-Warburton 2005) is considered to be part of this conceptual model depends on whether fungal species occurring on different host species interact. That a host filter can be an important consideration is made clear by reports of host-specificity (Molina et al. 1992; Ishida et al. 2007) and by a recent study by Dickie et al. (2010). They showed that when the non-native *Pinus contorta* invaded native *Nothofagus solandri* forest, the species of ectomycorrhizal fungi colonizing the pine were nearly all distinct from those colonizing the native tree. Obviously, the species of fungi colonizing the pine had to be present as immigrant propagules, but they could not be successful colonizers until the pine invaded.

The spatial scale of the community is important even within a single host species, as some have enormous geographical ranges that span large climatological gradients. The western North American tree Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), for example, ranges from western Canada, which receives relatively large amounts of rainfall, to central California, which receives relatively little rainfall (USDA NRCS Plants Database). The list of species of ectomycorrhizal fungi across the entire host range is undoubtedly much longer than that of a community in a small stand of Douglas-fir in central coastal California. Pinyon pine (*Pinus edulis*) grows on soils that vary markedly in moisture and fertility, and their ectomycorrhizal fungal communities may be quite distinct in the different soils (Gehring et al. 1998). Thus, if we consider a community to consist of interacting or, at least potentially interacting species, then we may need to consider the community to be more exclusive than "all species compatible with the host". It makes sense to consider a community of ectomycorrhizal fungi to be spatially defined by a single stand of trees, a single tree, or a portion of a single root system.

3 Defining species abundances

For communities of most organisms, it is relatively simple (at least in principle) to count or, at least, estimate the number of individuals in each species. For subterranean organisms, counting individuals is difficult because they are hidden from view. Moreover, it is difficult to define fungal individuals, and it is not even clear that the concept of individuals is relevant to fungi in all circumstances. A single genet of some fungal species may break apart into physically distinct ramets (Detman and van de Kamp 2001), and smaller ramets may anastamose to form larger ramets (Buchalo et al. 1989). Because the individual is ill-defined for most fungi, assessing species abundances is not particularly straightforward. Biomass is another measure of abundance but, of course, assessing biomass of subterranean mycelia is no more straightforward than assessing numbers of individuals. Therefore, frequency of occurrence in samples has been a method adopted by many fungal ecologists to express abundance. One must keep in mind, however, that the method used to assess abundance can certainly influence the perception of community structure (Lavorel et al. 2008).

4 The abiotic filter

Much of the structuring of biological communities can be explained by relating key functional traits to success along environmental gradients (Ackerly 2003; McGill et al. 2006). By its very nature, this approach is incapable of predicting the exact species present in a community. Instead, it seeks to predict the existence of particular phenotypes or functional types under particular abiotic conditions, irrespective of taxa. One must concede that such an approach is simplifying. Some will not recognize the approach as having anything to do with what we have traditionally called community ecology. But, in order to make any progress in our understanding of "intractably complex" communities, it seems essential to attempt a simplifying, trait-based approach to increase the likelihood of developing general principles that govern community structure.

This approach has not seen much use thus far by researchers of ectomycorrhizal fungal communities. However, the approach has been used by plant ecologists with some success. Consider, first, plants that fix CO_2 using either the C_3 carbon fixation pathway (C_3 plants), or a combination of both C_3 and C_4 carbon fixation pathways (C_4 plants, see Ehleringer and Monson 1993). A knowledge of both the distinct physiologies of C_3 and C_4 grass species (specifically the temperature sensitivity of quantum yield of photosynthesis) and summertime temperatures at various latitudes in the Midwestern USA allowed Ehleringer (1978) to predict that C_3 species should be photosynthetically superior to C_4 species at latitudes above 45°N, and C_4 species should be superior below 45°N. That prediction was consistent with the natural abundance pattern of grasses in the field. This example shows that the relative contributions to plant communities by C_3 and C_4 grasses can be predicted from knowledge of the interaction between an environmental factor and a plant trait. That this interaction is of general significance in determining the distribution of plants along temperature gradients is illustrated by the observation of similar patterns elsewhere in the world. For example, the distribution of C_4 sedges is related to a latitudinal gradient in Japan (Ueno and Takeda 1992), and the distribution of C_4 grasses is determined by an altitudinal gradient in Argentina (Cavagnaro 1988). In these examples, a functional type (in this case, photosynthesis type) can be predicted from an environmental variable (temperature), but the exact species cannot be specified. Thus, even an extensive catalog of plant species indicating whether they possess C_3 or C_4 photosynthesis could not indicate which species will occur in any location.

Other vegetation patterns also repeat themselves in different locations throughout the world with similar climates (Dansereau 1951), again demonstrating their general significance. Mooney et al. (1970) showed that, in California, along a moisture gradient from drier to wetter, one encounters first semi-arid scrub with succulents, semi-arid scrub, evergreen scrub and, finally, broad-leaf evergreen forest. That pattern of vegetation change was shown to be repeated in Chile where a similar moisture gradient occurs (Mooney et al. 1970). In Mediterranean climates, it is common to find shrubs and small trees with small, evergreen leaves possessing thick cuticles. Such leaves remain cooler and lose less water when stomata are closed than larger leaves possessing thinner cuticles. Dunn et al. (1976) showed that regions with Mediterranean climates throughout the world, whether in the Mediterranean itself, California, Chile, southwest Africa or southwest Australia, all possess similar vegetation characterized by shrubs and low trees with small, evergreen leaves possessing thick cuticles. In each of these cases, similar climates support vegetation possessing similar functional traits but with very different phylogenies (Mooney 1974).

More recently, Grime et al. (1997), Díaz et al. (2004) and Wright et al. (2004) have analyzed thousands of plant species from various parts of the earth. They found that, independent of geographic location and plant taxonomy, environmental gradients of decreasing water availability or decreasing soil fertility commonly result in a transition of communities comprising plants with the "fast and leaky" phenotype (typically with higher nutrient concentration, higher potential growth rate, lower leaf longevity, lower level of herbivore defense and rapid litter decomposition rates) to communities comprising plants with the "conservative/retentive" phenotype (typically with the opposite traits).

The utility of this general approach in understanding of the structure of a single community stems from observations of trait convergence (Grime 2006) or trait underdispersion (Pillar et al. 2009) of the taxa occupying only a small portion of the environmental gradient. In other words, species of a single community are predicted to possess common traits that adapt them to the same conditions. However, there may be multiple ways to cope with a particular environment. For example, in the desert, all plants need to cope with low levels of precipitation, but some desert plant communities comprise phraeatophytes, whose deep roots allow them to avoid water stress, shallow-rooted ephemerals that complete their life cycles during brief periods when adequate surface water is available, and shallow-rooted succulents that remain active year round by absorbing and storing water when it is available. Thus, functionally distinct ectomycorrhizal fungi may be able to coexist in dry habitats by disparate mechanisms including preferentially living deep in the soil where moisture is more available, producing rhizomorphs capable of transporting water from deep in the soil to shallower, drier portions of the soil, or surviving between periods of water availability as dormant spores. Because there may be more than one way to cope with low precipitation, some degree of trait variability may occur within the same community.

Nevertheless, abiotic filtering must occur to some extent. One does not expect to find in desert plant communities perennial species that are not either deeply rooted or succulent, and similar abiotic filtering must occur in communities of ectomycorrhizal fungi. Thus, the environment may filter a large, functionally variable pool of host-compatible species of ectomycorrhizal fungi on the basis of a particular functional trait. It is this abiotic filtering of traits that may serve to illustrate general principles of community structure.

Some of the potentially important environmental factors to consider when using this approach for ectomycorrhizal fungi are moisture, temperature, pH and nitrogen concentration because variation in each of these factors, irrespective of host species, appears to influence ectomycorrhizal fungal communities (Cavender-Bares et al. 2009; Rygiewicz et al. 2000; Koide and Shumway 2000; Lilleskov et al. 2001). You will note that two of these factors are resources for which organisms may compete (nitrogen, moisture), but the other two are not (temperature, pH). Some have distinguished between these two kinds of factors (Wilson 1999), but with respect to the effects of abiotic filtering, one need make no distinction. Each of these abiotic factors can filter functional traits that determine an organism's presence in a community. We use the term functional trait in the sense of environmental preferences and tolerances, but not resource requirements, which we assume to be the same for all members of the same ectomycorrhizal fungal community. The relevant functional traits possessed by the fungi that influence their success along gradients in these factors include preference for or tolerance to various levels of moisture, temperature, pH and nitrogen source. There are, undoubtedly, many more factors that could be considered, but these are probably among the most important factors that determine distributions of ectomycorrhizal fungi.

To illustrate how this works, consider a moisture gradient. Keep in mind that the gradient will always map to locations in real space but not necessarily to locations that are spatially contiguous. Let us assume that, because of its functional traits, species A is most successful in a position along the gradient characterized by low moisture. It therefore occupies the driest portion of the gradient. It does not occupy other positions with greater water availability because, presumably, its physiology does not allow it to be successful in other portions of the gradient due to trade-offs so commonly observed (Tilman 1990). Other species populate the wetter portions of the gradient because their physiologies are better suited to greater moisture availabilities.

There are now many examples of isolates of ectomycorrhizal fungi differing from each other in various functional traits that we assume affect their success along moisture, temperature and other environmental gradients. For example, species of ectomycorrhizal fungi are known to differ from each other substantially in drought tolerance (Mexal and Reid 1973; Coleman et al. 1989; Jany et al. 2003). Ectomycorrhizal fungal isolates also differ from one another in preference for substrate pH (Hung and Trappe 1983; Sundari and Adholeya 2003), temperature (Hacskaylo et al. 1965; Theodorou and Bowen 1971; Cline et al. 1987; Tibbett et al. 1998) and in tolerance to freezing (France et al. 1979).

Currently, the only known use of this approach as applied to ectomycorrhizal fungal communities concerns distributions of taxa along N availability gradients. The structure of ectomycorrhizal fungal communities clearly varies along N availability gradients (Kranabetter et al. 2009). Is this because functional trait differences among species of ectomycorrhizal fungi that relate to N nutrition determine distributions in space? Taylor et al. (2000) and Lilleskov et al. (2002) independently studied ectomycorrhizal fungal communities along N deposition gradients in Europe and Alaska, respectively. Lilleskov et al. (2002) located study sites along an atmospheric N deposition gradient caused by a fertilizer manufacturing plant on the Kenai Peninsula. Nitrogen deposition varied 20-fold along the gradient. Ectomycorrhizal fungi from the various sites were cultured from sporocarps or root tips. All the isolates were able to use ammonium as an N source, but only fungi from sites with low availability of mineral N grew well on protein. Those from high N sites did not. Taylor et al. (2000) studied communities of ectomycorrhizal fungi associated with Norway spruce (*Picea abies*) along an N deposition gradient from Scandinavia (relatively pollution free) to central Europe. Again, isolates from low N sites grew better on protein than did those from more N-polluted sites. The general principle seems to be that, irrespective of taxa, when the major pool of N is organic (protein) and mineral N is poorly available, an increased capacity to utilize protein as an N source results in greater success.

These studies predict variation in protease activity along gradients of mineral N availability (Fig. 1). So, for a community existing along a portion of this gradient characterized by moderately low mineral N availability as indicated by the wide bar (Fig. 2), species A is most abundant and species C is least abundant. At a position of moderately high mineral N availability, the species abundances would occur in the reverse order. These studies also predict that, within a given community, there will be a convergence of protease activity among coexisting species (Fig. 3). Again, such an approach does not allow one to predict the specific taxa that will occur, but it does allow one to predict how, for any taxon, success along the gradient relates to the expression of a key functional trait.

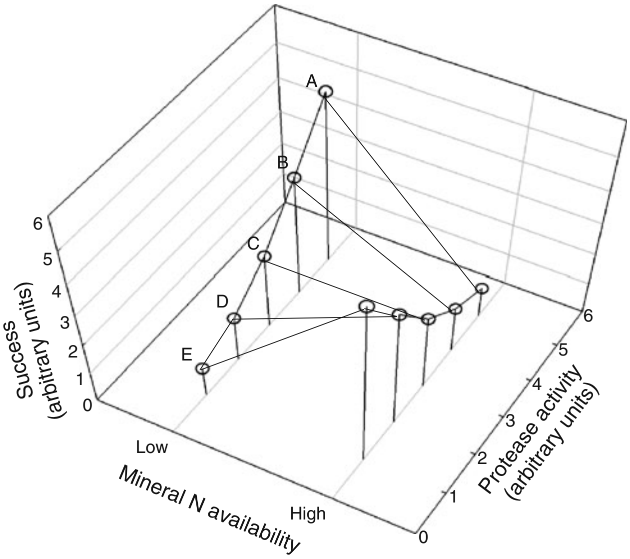

Fig. 1 Theoretical relationship between mineral N availability (the environmental gradient), protease activity (the functional trait), and some measure of success for five hypothetical species of ectomycorrhizal fungi based on results from Taylor et al. (2000) and Lilleskov et al. (2002)

5 Competitive exclusion

Many ecologists have shown that competition can be an important factor in structuring biological communities (Bengtsson et al. 1994). In a sufficiently homogeneous habitat, interspecific competition may lead to a reduction in evenness (Lamb et al. 2009) or, at the extreme, the exclusion of some species from the community (Grace and Wetzel 1981). Some have considered competitive interactions to be a type of "biotic filtering". The term "filter" implies that some taxa or traits are in the process of being kept out, but competition can only occur among species that are present in the community. Thus, competitive exclusion should not be considered a filtering process, per se.

Presumably, one species is more competitive than another, not because it is similar in all respects to the second, but because it is different in some ecologically relevant trait that results in competitive superiority. Species must be similar in resource requirements in order for competition to occur, but it is some difference in acquiring the resource that makes one taxon more competitive than the other. In terms of carbon capture, species A may be more competitive than species B simply because, when new roots become available, it colonizes so many of them that there are not enough roots left to maintain species B. Competition for carbon has not been demonstrated explicitly among species of ectomycorrhizal fungi, but competition for uncolonized root tips can be clearly demonstrated in pots and in microcosms (Wu et al. 1999; Kennedy et al. 2009), and evidence for competition also occurs in the field (Pickles et al. 2010). Koide et al. (2005b) found that the spatial distributions of hyphae of ectomycorrhizal fungi in the forest floor of a pine plantation was non-random and, in some cases, suggestive of competition for resources found in the soil.

Competition is frequently context-dependent (Erland and Finlay 1992; Mahmood 2003) because the resource competed for will vary from place to place and time to time. Nevertheless, general principles can probably be developed that help us understand how it acts to structure communities. Unless there is a significant degree of saprotrophy, the ability to colonize a root and maintain possession of it must be important in determining competitive hierarchies for carbon capture. In terms of other resources, such as N or P or water, the ability to colonize soil volume and maintain possession of it must be important in determining competitiveness for those resources. Thus, traits such as growth rate, antibiosis (Krywolap 1964), or the minimum concentration of a resource at which it can still be acquired (Tilman 1981) may determine competitive ability. It stands to reason that the most abundant species in a community will be those that are

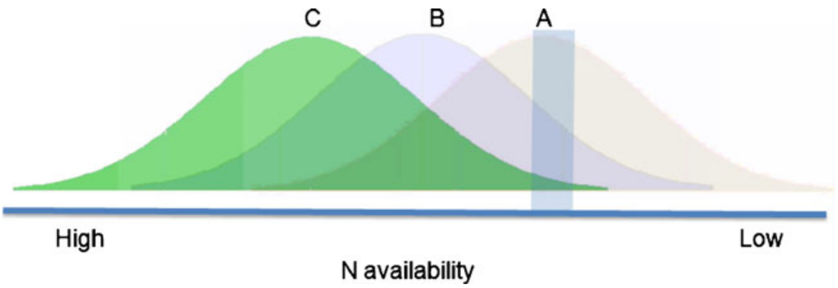

Fig. 2 As a result of variation in protease activity (the functional trait, see Fig. 1), different species exhibit unique distributions along a mineral N availability gradient. The vertical axis is a measure of success (abundance, etc.). For a community existing along a portion of this gradient (as indicated by the *wide*, *vertical* bar), species A is most abundant and species C is least abundant. At the higher end of the mineral N availability, the reverse would be true

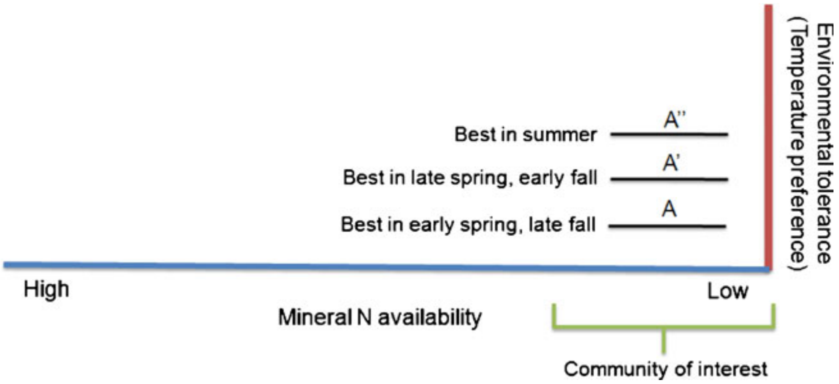

Fig. 3 Assume that species A, A′ and A″ are functionally redundant in the sense that they all possess high protease activity (a functional trait). Thus, they can each exist in the same community characterized by low mineral N availability. Competitive exclusion does not occur because the species differ significantly in temperature preference (another functional trait). Species A may prefer the coolest temperatures and so is the most competitive species in the early spring or late fall. Species A′ may prefer intermediate temperatures and so is the most competitive in late spring or early fall. Species A″ may prefer the warmest temperatures and so is the most competitive in summer. Thus, as the seasons change (resulting in temporal heterogeneity of the habitat), first one species and then another will tend to become dominant, but none will permanently gain the upper hand

the most competitive for some limiting resource and, therefore, that the traits determining the capture and maintenance of roots and soil volume are critically important. Thus far, however, little is known about the relationship between such traits and community dominance.

6 Coexistence

Disturbance The effects of competitive interactions can be ameliorated or, in other words, the coexistence of multiple species may be facilitated by at least two common phenomena. First, communities may be prevented from attaining equilibrium because of discrete events that prevent the more competitive species from excluding the less competitive (Pickett 1980; Brokaw and Busing 2000; Grime 2006) such as disturbance or the continual creation of new resource. One such example for ectomycorrhizal fungi is the production of new roots (Bruns 1995).

New roots can be produced in two ways. Existing trees produce new roots from existing roots. New roots can also be produced de novo by recruiting seedlings. In some communities, colonization of seedlings by ectomycorrhizal fungi is accomplished primarily by the species already present on adult host plants nearby (Dickie et al. 2002a). Therefore, the communities developing on new seedlings would normally be very similar to the communities found on the surrounding adults. But, in the *P. edulis* system of northern Arizona (Gehring et al. 1998), a large degree of variation exists among individual trees in the structure of the ectomycorrhizal fungal community. This pattern may be a consequence of the inability of the ectomycorrhizal fungi of adult hosts to colonize new seedlings, perhaps due to dry conditions or large inter-plant spacing, which necessitates new immigration for each new seedling. In any case, this observation suggests that, in some systems, another source of fungal diversity, another community structuring force, may simply be continuous seedling recruitment.

The nature of disturbance may determine the traits that determine the outcome of competition. In a habitat characterized by frequent disturbance, rapid growth may be a more competitive strategy than slow growth by virtue of being able to more readily colonize disturbed patches. However, in undisturbed habitats, just the opposite might be expected if the slow-grower is able to capture resources previously controlled by the faster grower. For example, Wu et al. (1999) found that *Pisolithus tinctorius* was a fast grower, which may make it superior in frequently disturbed habitats, but they also found that, in the absence of disturbance, it was eventually outcompeted by a slower-growing species. Therefore, the traits that determine competitive outcomes may depend on the nature of disturbance.

Habitat partitioning Even in the absence of disturbance, habitat heterogeneity (in space or time) coupled with appropriate trait dissimilarity allowing the taxa to exploit that heterogeneity can lead to habitat partitioning. Habitat partitioning may reduce the frequency or intensity of competitive interactions and thus contribute to species coexistence and the maintenance of diversity within communities, just as disturbance does. There are now several studies that suggest that habitat partitioning plays a role in maintaining diversity in communities of ectomycorrhizal fungi. In the red pine (*Pinus resinosa*) plantation where we have worked for some time, the most commonly occurring fungi as mycorrhizas include *Cenococcum geophilum*, *Lactarius oculatus*, *Tylopilus felleus*, *Clavulina cinerea* and *Russula* sp. These species are not only common; they have a rather uniform frequency distribution (Koide et al. 2005a). Rather, even species distributions have been found in other communities (Taylor 2002). Even frequency distributions do not seem likely if competition strongly structured the community (Lamb et al. 2009). But, coexistence may be facilitated by habitat partitioning. First, spatial partitioning occurs. The hyphae of the dominant fungi are located in different layers of the forest floor (Dickie et al. 2002b); *Cenococcum* and *Clavulina* had similar distributions but those differed from the distributions of *Lactarius* and *Tylopilus*, which had similar distributions. And, distributions of *Lactarius* and *Tylopilus* differed from that of *Russula*. Moreover, while *Cenococcum* and *Clavulina* were both distributed in similar layers of the forest floor, the two species tended not to exist in the same small volume of substrate (Koide et al. 2005b). Other evidence of spatial partitioning was presented for ectomycorrhizal communities in *P. abies* stands by Baier et al. (2006) and Scattolin et al. (2008), in a mixed conifer forest by Rosling et al. (2003), in a mixed *Quercus* forest by Courty et al. (2008), and in a *Quercus rubra* forest by Gebhardt et al. (2009). Second, temporal partitioning occurs. We found that *Lactarius* and *Tylopilus* exhibited similar temporal patterns, but those were distinct from another temporal pattern exhibited commonly by *Cenococcum*, *Clavulina* and *Russula* sp (Koide et al. 2007). Courty et al. (2008) also found evidence of temporal partitioning in a *Quercus* forest. The relevant traits that may contribute to habitat partitioning (either spatial or temporal) in a heterogeneous habitat include those traits that influence success under the varied conditions of the patchy habitat. For example, if the habitat is heterogeneous with respect to pH, tannin concentration, oxygen concentration, temperature, moisture or nitrogen source, then variation in preferences for pH, tannin concentration, oxygen concentration, temperature, moisture and nitrogen source will be the traits that determine the extent of habitat partitioning and, therefore, the extent of amelioration of competitive interactions.

Habitat partitioning in response to habitat heterogeneity may occur as a consequence of divergence of various traits that are different from the trait that was originally filtered by the abiotic factor. For example, let us assume that the abiotic filter required that all species possess a high protease activity. Thus, species A, A′ and A″ are functionally similar in that they all possess some minimum protease activity. Let us further assume that each species differs substantially in terms of temperature preference; species A prefers the coolest temperatures and so is the most competitive species in the early spring or late fall, species A′ prefers intermediate temperatures and so is the most competitive in late spring or early fall, and species A″ prefers the warmest temperatures and so is the most competitive in summer. Thus, as the seasons change, first one species and then another will tend to become dominant, but none will permanently gain the upper hand (Fig. 3). The convergence in protease activity explains the presence of all

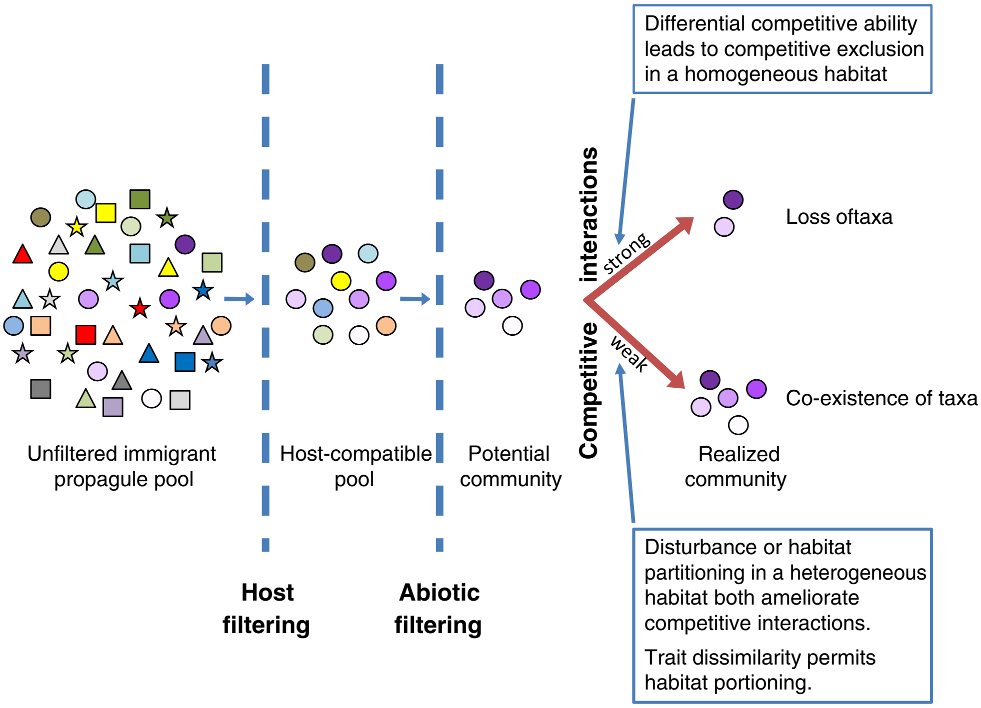

Fig. 4 A graphical representation of the hierarchical community structure model. Each combination of shape and color represents a unique taxon. Variation in shape represents variation in host compatibility. Taxa forming the realized community must tolerate filtering of traits by host species, filtering of traits by the abiotic environment, and the effects of some level of competitive interaction. Competitive hierarchies due to trait variation in a homogeneous community may ultimately lead to exclusion, but competition may be ameliorated to varying degrees by disturbance or habitat partitioning, leading to varying degrees of coexistence. Habitat partitioning depends on trait variation in a heterogeneous habitat

three at the same position along the N availability gradient (and thus their presence within the same community), and the difference in terms of temperature preference, coupled with recurring seasonal changes in temperature, insures the constant disruption of competitive hierarchies and thus explains coexistence.

If temperature were to change in a directional manner, such as a steady warming, the species that is adapted to the warmer conditions (species A″, Fig. 3) may begin to competitively exclude another that is adapted to cooler conditions (for example, species A). Thus, while coexistence was previously maintained by a particular regime of seasonally shifting temperature, at elevated temperatures, the functional traits may become mismatched with the new temperature regime, and a reorganization of the community might be the consequence. The point to make here is simply that, if a climate factor either determines initial filtering or contributes to habitat partitioning, change in climate is expected to structurally modify the community (see Cox et al. 2010).

The foregoing discussion suggests that the structure of communities must frequently depend on more than a single functional trait. One trait may be subject to the primary abiotic filtering mechanism. Another may influence competitive outcomes. Still, another may be responsible for ameliorating competition. Obviously, one could theoretically employ an infinite number of dimensions (Hutchinson's *n*-dimensional "hypervolume", Hutchinson 1957) to explain 100% of community structure; presumably, a taxon could be uniquely identified by the intersection of a sufficient number of functional axes. Obviously, that level of detail may never be attainable but neither is it particularly desirable, for the goal here is not to produce rules of community assembly that predict particular species abundances. Indeed, it is quite instructive to consider the fact that one can predict broad vegetation types ("formations") throughout the world (tropical rainforest, temperate forest, grassland, tundra, etc.) based on only two axes: temperature and precipitation (Dansereau 1951). A simplifying approach involving a limited number of axes seems desirable if we are to make progress in understanding community structure.

7 Conclusions

We propose a conceptual hierarchical model of ectomycorrhizal fungal communities (Fig. 4). Whether a "host filter" is considered to be part of this conceptual model depends on whether fungal species occurring on different host species interact. In addition to a potential host filter, the abiotic environment acts as a filtering mechanism. Another part of the model concerns competitive interactions and the factors that reduce it, including disturbance and habitat partitioning. Competitive exclusion occurs as a consequence of competitive hierarchies resulting from variation in traits relevant to the acquisition of limiting resources. The response to disturbance depends on variation in functional traits. Finally, the exploitation of a heterogeneous habitat to produce habitat partitioning also depends on variation in functional traits. Some may object to this approach because it focuses on traits rather than on taxa. Thus, the approach is not capable of predicting community structure, per se, if species identity is a component of community structure. For that reason, many may consider the approach to be outside the bounds of traditional community ecology. But, this trait-based approach may prove to be more useful in producing general principles concerning the structuring of communities of ectomycorrhizal fungi than have yet emerged from the many traditional, taxon-based studies. It may prove to be of some use in conservation, habitat restoration, prevention or amelioration of species invasions, and the prediction of responses to climate change.

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