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The Mutualistic Niche: Mycorrhizal Symbiosis and Community Dynamics

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Abstract

The niche is generally viewed in terms of species' intrinsic physiological potential and limitations due to competition. Although DNA sequencing has revealed the ubiquity of beneficial microbial symbioses, the role of mutualisms in shaping species niches is not broadly recognized. In this review, I use a widespread terrestrial mutualism, the ectomycorrhizal symbiosis, to help develop the mutualistic niche concept. Using contemporary niche theory, I show how mycorrhizal symbioses expand environmental ranges (requirement niche) and influence resource use (impact niche) for both plants and fungi. Simple niche models for competition between resource specialists and generalists also predict a range of ecological phenomena, from unexpected monodominance by some tropical trees to the functional biogeography of mycorrhizal symbiosis. A niche-based view of mutualism may also help explain stability of mutualisms even in the absence of clear benefits. The niche is a central concept in ecology, and better integration of mutualism will more accurately reflect the positive interactions experienced by nearly all species.

Mutualism:

a cooperative relationship between species based on mutually beneficial interactions, such as the reciprocal exchange of resources or services

Symbiosis: the living together of different species in intimate associations that range from mutualism to parasitism

Arbuscular mycorrhiza:

mycorrhiza formed by fungi in the Glomeromycota and characterized by formation of branched structures (arbuscules) within root cells. It is the ancestral and most common form of mycorrhizal symbiosis

Ectomycorrhiza:

mycorrhiza distinguished by a sheath of fungal tissue totally encompassing plant terminal roots. It evolved at least 150 Mya and involves a diverse range of Basidiomycota and Ascomycota fungi with saprotrophic ancestors

Ericoid mycorrhiza:

mycorrhiza formed by plants in the family Ericaceae and fungi predominately from the orders Helotiales and Sebaciales. It evolved at least 80 Mya and is characterized by the formation of fungal coils within root cells

1. MUTUALISM IN ECOLOGY: A CHANGED PARADIGM

Although the potential for mutually beneficial cooperation between species (hereafter mutualism) (West et al. 2007) was recognized early in the history of biology (De Bary 1879), ecologists for many years considered the phenomenon to be uncommon (Rich & Boucher 1976). As a result, research on ecological interactions historically focused on antagonisms such as natural enemies and competition, leaving the consequences of mutualisms relatively unexplored (Boucher et al. 1982). Since Boucher, physiological studies have repeatedly demonstrated the beneficial nature of widespread interactions, such as mycorrhizal symbiosis (Smith & Read 2008), and key conceptual papers have framed the potential impacts of mutualisms and other positive interactions on ecological communities (Bertness & Callaway 1994, Bruno et al. 2003). In addition, technical advances in DNA sequencing, in conjunction with other tools, have greatly facilitated investigation of communities of cryptic organisms, such as bacteria and fungi (Horton & Bruns 2001), and have rapidly expanded the known incidence and variety of mutualistic interactions (Marquez et al. 2007, Partida-Martinez & Hertweck 2005). Thus, despite an early focus on negative interactions, mutualisms are now widely recognized as common and important.

Accumulating evidence for the importance of mutualism has driven several attempts to understand how mutualism impacts ecological systems. These studies have looked through the lenses of functional traits (Friesen et al. 2011), market theory (Schwartz & Hoeksema 1998), and food webs (Holland et al. 2013). Although the niche concept has been a cornerstone of ecological theory for many years (Chase & Leibold 2003, Chesson 2000, Grinnell 1917, Hutchinson 1957, MacArthur 1958), thereby helping to identify the factors controlling species distributions and predict the outcome of interactions with other species (Holt 2009, Pulliam 2000), integration of mutualism lags behind other areas of niche theory (Chase & Leibold 2003). Some theory has applied niche concepts to mutualistic systems (Bever et al. 2010, Bruno et al. 2003, de Mazancourt & Schwartz 2010), and a small but growing number of empirical studies examine the impact of mutualism on species niches (Afkhani et al. 2014, Elias et al. 2008, Kazenel et al. 2015, Warren et al. 2010); however, the prevalence of mutualism and the centrality of niches in ecological theory calls for greater integration of the two topics.

From this perspective, mycorrhizal symbiosis—which involves reciprocal complementary resource exchange between plant roots and soil-dwelling fungi—provides an excellent opportunity to synthesize progress in niche theory with the rapidly accumulating empirical data on communities of cryptic organisms, such as fungi and bacteria. Mycorrhizal symbiosis evolved nearly 500 Mya and represents the ancestral condition for most plants, as it occurs in ~80% of all extant species (Brundrett 2009, Field et al. 2015, Redecker et al. 2000). Along with lichens and pollinators, mycorrhizal symbiosis represents one of the great terrestrial mutualisms. Multiple forms of mycorrhizal symbiosis have evolved over the past 500 Mya, such as arbuscular mycorrhizas, ectomycorrhizas, and ericoid mycorrhizas, generally involving distinct anatomies and plant and fungal partners (Smith & Read 2008, van der Heijden et al. 2015). Although I discuss all three forms, I center discussion on ectomycorrhizas as they represent the first major departure from the ancestral arbuscular mycorrhizal state, they occur in many dominant temperate and tropical tree families, and the evolution of ectomycorrhizal fungi from multiple wood-decomposing lineages has a unique impact on their mycorrhizal niche.

In addition to synthesizing current literature on the mycorrhizal niche, I also apply the theoretical framework of contemporary niche theory (CNT) (Chase & Leibold 2003) to develop explicit models of how mycorrhizal mutualism affects plant and fungal niches and show how these models can be used to explain a variety of ecological patterns. This approach should be generalizable to many mutualistic systems, such as corals, pollinators, legume rhizobia, and fungal endophytes, and my goal is to stimulate further interest in mutualistic niche models.

2. THE MUTUALISTIC NICHE

The niche concept has been variously defined during its long history in ecology: the specific habitats a species occupies (Grinnell 1917), an abstract N-dimensional hypervolume circumscribing the environmental conditions necessary for a species to practice its way of life (Hutchinson 1957), or the ecological role a species plays within a community or ecosystem (Elton 1927). Although a species' niche should predict where it can be found in nature, Hutchinson recognized that species occupy only a subset of their potential (or fundamental) niche space and termed this phenomenon the realized niche (Hutchinson 1957, Pulliam 2000) (**Figure 1a**). Most commonly, the fundamental niche is defined in terms of abiotic properties of the environment (Pulliam 2000, Warren et al. 2014), and the realized niche is defined as the outcome of negative biotic interactions (e.g., competition, predation) with other species, although dispersal limitation may also lead to unoccupied niche space (Hargreaves et al. 2014, Pulliam 2000).

Mutualisms complicate the traditional niche concept because much of what is generally considered part of a species' fundamental niche may have been made by mutualistic interactions (**Figure 1a**). Empirical examples from mycorrhizal symbiosis include numerous situations in which the absence of fungi prevents their plant hosts from colonizing what would otherwise be considered suitable habitat, and vice versa (Nunez et al. 2009, Weber et al. 2005). Using the conventional terminology, either the fundamental niche implicitly includes mutualism and other positive interactions, or the realized niche is often larger than the fundamental niche (Bruno et al. 2003). To facilitate discussion of these different components of the niche, I use the individualistic niche to distinguish the N-dimensional set of environmental conditions in which a species can maintain a population in the absence of all biotic interactions, including mutualist partners and competitors, and the mutualistic niche as the full set of environmental conditions in which a population can be maintained in the presence of mutualist partners but in the absence of antagonistic biotic interactions (**Figure 1a**). Because occupation of suitable parts of mutualistic niche space may still be limited by antagonistic interaction with other species, the realized niche is the net result of both positive and negative interactions. Although any arrangement of the individualistic and mutualistic niches is possible, the capacity to expand niche space is likely a common feature of many facultative and obligate mutualisms (but see Warren et al. 2010 for a counterexample). For example, mycorrhization enables host plants to increase growth at lower levels of soil phosphorus (**Figure 1b**), and facultative endophytic fungi enable host plants to grow in hotter environments (Marquez et al. 2007) and expand their range into drier climates (Afkhani et al. 2014). Although I expect that in many cases the individualistic niche lies entirely within the mutualistic niche, the individualistic niche may extend beyond the mutualistic niche in cases with significant costs or trade-offs associated with the mutualism, such as plants in a shady environment when the mutualism has a high carbon cost. There is some evidence of such context-dependent benefits for mycorrhizal symbiosis, with mycorrhizal fungi having net costs to their plant hosts in high-nutrient environments (Johnson et al. 2010) (**Figure 1b,c**).

Individualistic niche:

the potential niche space in which a species could maintain a population in the absence of biotic interactions, including mutualist partners

Mutualistic niche:

the potential niche space in which a species could maintain a population in the presence of mutualist partners

2.1. A Contemporary Niche Approach to Mutualism

Despite the potential for mutualistic niche expansion, relatively few studies have quantified the effect of mutualism on niche dimensions, perhaps in part due to the ambiguity involved in defining a niche. One useful framework in this respect is the CNT proposed by Chase & Leibold (2003), which defines the niche with respect to the minimum environmental conditions necessary to maintain a population (requirement niche) and the effect of an organism on those environmental conditions (impact niche). This framework not only can be mapped back to classic niche concepts

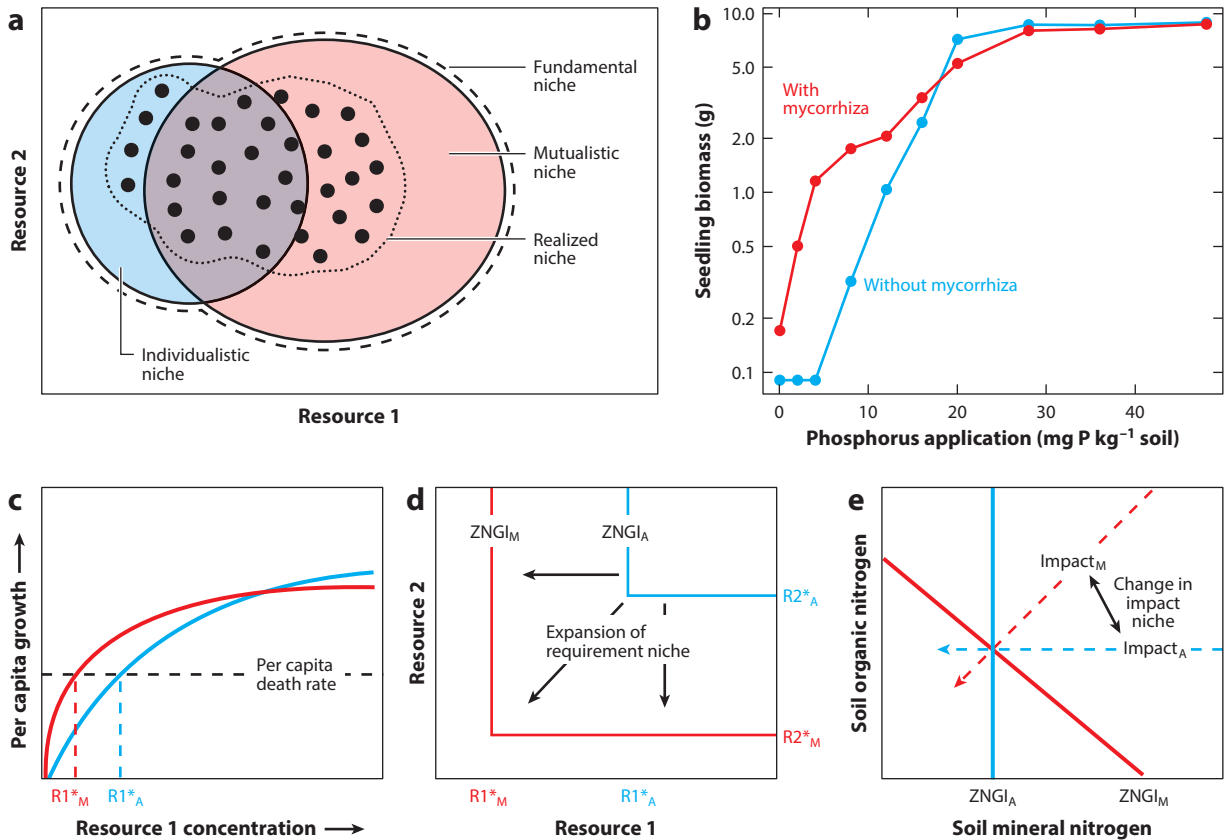


Figure 1

Defining the mutualistic niche. (a) Hutchinson's fundamental niche (dashed line) and realized niche (dots within dotted line) distinguish potentially suitable and occupied niche space, respectively. Panel a illustrates the possible contribution of mutualism (red) to what is generally considered fundamental niche space. (b) Growth rate for ectomycorrhizal (red) and nonmycorrhizal (blue) *Eucalyptus* seedlings across a phosphorous fertilization gradient. (Data in panel b from Bougher et al. 1990). (c) A population model generalizing results from panel b that illustrates the proposed effect of the phosphorus gradient, now termed resource 1 concentration, on per capita birth and death rates in the presence (red) and absence (blue) of mycorrhiza. This model can be used to determine the minimum resource requirements (R^*) of a species growing in mycorrhizal symbiosis (R^*_M , red) versus those growing alone (R^*_A , blue). Importantly, the model works for either partner—in other words, a plant growing with or without its mycorrhizal fungus or a fungus growing with or without its mycorrhizal host plant. (d) R^* can be quantified for multiple resources and used to predict how mycorrhizal symbiosis expands the requirement niche. Lines show how mutualism could expand the niche by shifting from the $ZNGI_{\text{Alone}}$ ($ZNGI_A$) to the $ZNGI_{\text{Mutualism}}$ ($ZNGI_M$), on the basis of the R^* for each of two essential nonsubstitutable resources, such as nitrogen and phosphorus. (e) Resource consumption (impact niche) may also change as a result of mutualism. Dashed arrows represent consumption vectors showing the trajectory along which resources will be drawn down for a species alone (Impact_A) or with a mutualist partner (Impact_M). In this example, mycorrhizal mutualism enables plant consumption of organic nitrogen (red arrow, Impact_M); in contrast, nonmycorrhizal plants can access only mineral nitrogen (blue arrow, Impact_A). The diagonal red $ZNGI_M$ line indicates that the two resources are substitutable for the mycorrhizal plant. Abbreviation: ZNGI, zero net growth isocline.

(e.g., fundamental and realized niche) but also incorporates the resource competition models developed by MacArthur (1972) and generalized by Tilman (1976, 1980, 1982), which have proved highly successful in predicting the outcome of species interactions (Miller et al. 2005). Because CNT provides a clear framework for quantifying niche dimensions and predicting the outcome of species interactions, it is particularly useful in testing hypotheses about the mutualistic niche.

The requirement niche can be defined by first identifying the minimum level of a limiting essential resource that is necessary for a given species to maintain a population (**Figure 1c**). Above this minimum resource level, also known as R^* , per capita birth rate exceeds per capita death and the population grows, whereas the reverse occurs below R^* (Tilman 1976, 1980, 1982). For two limiting essential resources, the R^* expected at equilibrium can be used to draw an isocline of zero net population growth within a state space defined by these essential resources (**Figure 1d**). The requirement niche is then defined as the area of this state space including and above the population zero net growth isocline (ZNGI); within this niche resources are sufficient to maintain a population. In this sense the requirement niche is similar, although not identical,¹ to Hutchinson's niche concept in that it delineates conditions necessary for a species to fulfill its way of life. Using this framework, the impact of mutualism on a species' niche can be measured explicitly by estimating R^* with and without the mutualism (R^*_M versus R^*_A in **Figure 1c**), as well as the corresponding changes in boundaries of the requirement niche in resource state space (ZNGI_M versus ZNGI_A in **Figure 1d**). When directly measuring per capita fitness and death rates is not possible (as in long-lived tree species), suitable reaction norms must be developed as proxies for R^* (e.g., the use of plant biomass in **Figure 1b**).

The second niche component, the impact niche, describes the effect a species has on its environment. Using the state space developed above to depict the requirement niche, an impact niche that describes how an organism's consumption changes the concentration of limiting resources can be defined. At the population equilibrium defined by R^* , a species per capita impact on a single resource is equal to the ratio of the density-independent death rate of the consumer (d) to the efficiency with which the resource is converted into new individuals (a), or d/a (Chase & Leibold 2003, p. 23). For any initial starting concentration, or supply point, of these two resources within the requirement niche, population growth will reduce resource concentrations as the sum of the independent consumption vectors for each resource. The impact niche can be depicted in state space as a consumption vector passing through the system equilibrium, along which resource concentrations decline until the system reaches the equilibrium defined by the population growth ZNGIs. Here again, the impact of mutualism can be quantified directly as a change in the vector describing the impact niche (Impact_{Mutualism} versus Impact_{Alone} in **Figure 1e**). Another critical component of CNT is the resource supply point, which is the equilibrium concentration of resources in the absence of the organism(s) being modeled. Although the emphasis here has been on resources, one advantage of CNT is that niche components can be generalized to include factors other than resources, such as environmental stress, predators, herbivores (Chase & Leibold 2003, Chase et al. 2000), and mutualists.

2.2. The Mycorrhizal Requirement Niche

Good evidence that mycorrhizal symbiosis expands key axes of the plant and fungal requirement niches has been found. In ambient environmental conditions, where soil nutrients are often limiting, adding ectomycorrhizal fungi improves plant performance as measured by most growth metrics, including biomass accumulation, tissue nutrient concentrations, and survival (Nara & Hogetsu 2004, Smith & Read 2008). When studies have compared growth of seedlings across a resource availability gradient with and without ectomycorrhizal fungi (e.g., Bougher et al. 1990), symbiosis leads to large increases in plant growth, particularly at low levels of soil nutrient

¹For CNT models of two competing species (Section 3), the requirement niche may be quantified in the presence of all species other than the two being modeled, in which case it is not strictly the fundamental niche.

availability (**Figure 1b**), consistent with a lowering of R^* and expansion of the requirement niche (as depicted in **Figure 1c,d**). Although most ectomycorrhizal growth studies are not directly linked to per capita birth or death rates because the hosts are generally long-lived trees, evidence of failed plantations in the absence of ectomycorrhizal fungal inoculum suggest that linking these reaction norms to population processes is not unreasonable (Pryor 1956).

Fungi increase plant nutrient uptake by several mechanisms. Most familiar is the greater surface-to-volume ratio of fungal hyphae. However, fungi also produce a diverse array of strong degradative enzymes (Lindahl & Tunlid 2015, Talbot et al. 2015) with advantageous Michaelis-Menten kinetics for nutrient uptake. For example, in pure culture, plant roots generally have lower maximum uptake (lower V_{\max}) and are less efficient at low nitrogen concentrations (higher K_m) than microbes (Kuzuyakov & Xu 2013). In contrast, direct measurements of mineral and organic nitrogen uptake show that mycorrhizal roots have high V_{\max} and low K_m uptake systems that are comparable with those of saprotrophic microbes (Wallenda & Read 1999). Although the ability of mycorrhizal fungi to act as decomposers has been a topic of some debate (Talbot et al. 2008), one area of recent progress has been confirmation that many ectomycorrhizal fungal species produce oxidative enzymes related to the ligninolytic capabilities of their saprotrophic ancestors (Shah et al. 2016). This decomposing ability likely explains the increasing range and complexity of organic compounds that ectomycorrhizal plants can use as primary nitrogen sources (Turnbull et al. 1995) and is thought to be among the primary benefits of associating with ectomycorrhizal fungi (Terrer et al. 2016).

Mycorrhizal symbiosis effectively lowers the fungal requirement for soil environmental carbon ($R^*_{\text{Env. Carbon}}$) to zero. Access to plant photosynthate expands the fungal requirement niche by allowing mycorrhizal fungi to grow when soil organic carbon is otherwise unavailable to them, either for competitive or environmental reasons. Although saprotrophic microbes may access carbon from living root exudates or from decomposing plant litter, ectomycorrhizal fungi receive an estimated 7–30% share of net primary productivity (Leake et al. 2004) and ectomycorrhizal mycelium often dominates fungal biomass in nature (Wallander et al. 2001), which suggest that ectomycorrhizal symbiosis is highly advantageous for fungi. Further, even ectomycorrhizal fungi with litter-degrading enzymes assimilate little if any carbon through saprotrophy (Lindahl & Tunlid 2015).

The ability of both mycorrhizal plants and fungi to associate with multiple partners may also contribute to mutualistic niche expansion. For example, ectomycorrhizal fungal species have been shown to vary in their ability to target different nutrients, such as nitrogen and phosphorus, or organic and mineral forms of the same nutrient (Courty et al. 2010). Thus, the ability to associate with multiple partners with varying functionality should enable expansion of the requirement niche along multiple axes.

2.3. The Mycorrhizal Impact Niche

Symbiosis between plants and ectomycorrhizal fungi alters resource consumption in ways that distinctly modify the environments in which they occur. Although some plants can directly take up simple organic nitrogen sources (such as the amino acid glycine), plants associated with ectomycorrhizal fungi receive a greater fraction of their nitrogen from organic sources (Turnbull et al. 1995), which shifts their impact niche (**Figure 1e**). Resource consumption ratios may also change, as plant tissue stoichiometry responds to mycorrhizal colonization (Güsewell 2004). Mycorrhizal association can also affect fungal impacts on resources. To meet host demand, ectomycorrhizal fungi take up more nitrogen than free-living saprotrophs. Ectomycorrhizal fungi also immobilize large quantities of soil nitrogen, even when it is not passed on to the host (Koide & Kabir 2001,

Nasholm et al. 2013). Some mycorrhizal fungi, such as *Pisolithus*, use significantly different nitrogen sources in pure culture than in symbiosis (Turnbull et al. 1995), and in one study adding glucose to mimic host carbon stimulated the transcription of genes associated with degradative enzyme production and nitrogen uptake in the ectomycorrhizal fungus *Paxillus involutus* (Rineau et al. 2013). Finally, significant differences among enzymatic activities (Courty et al. 2005, Walker et al. 2014) and functional traits (Koide et al. 2014) of ectomycorrhizal fungi may make plant resource consumption dependent on ectomycorrhizal partner identity.

Because the resources traded between mycorrhizal partners (carbon, nitrogen, phosphorus) directly influence several of the most important biogeochemical cycles, these interactions have received increasing attention in ecosystem and global change ecology. For example, recent studies have shown that accumulation of carbon and nitrogen differ significantly in forests dominated by ectomycorrhizal trees compared with those dominated by arbuscular mycorrhizal trees (Averill et al. 2014, Phillips et al. 2013) and that ectomycorrhizal fungi significantly affect patterns of soil development (Clemmensen et al. 2013). Ectomycorrhizal trees are also better able to overcome nitrogen limitation in the face of elevated atmospheric CO₂ (Terrer et al. 2016). Microbial communities have long been known to regulate key biogeochemical cycles (Falkowski et al. 2008), but the particular ways in which mycorrhizal mutualism alters patterns of plant and fungal resource use may be more important for biogeochemical cycles than previously suspected.

3. COMMUNITY DYNAMICS IN THE LIGHT OF MYCORRHIZAL MUTUALISM

Elucidating the ecological mechanisms underlying patterns of community composition lies at the root of much of modern ecology (Cowles 1899, Whittaker 1956). Although the growth-promoting abilities of mycorrhizal associations have long been recognized (Frank 1885, as translated in Frank 2005), ecological explanations for plant community dynamics have tended to ignore microbial influence (Bever et al. 2010, Hodge et al. 2013). In this section, I use the mutualistic niche concept to synthesize evidence that ectomycorrhizal mutualism contributes to coexistence, competitive exclusion, and facilitation in plant and fungal communities.

3.1. Mycorrhizas and Plant Coexistence

Niche-based theories require coexisting organisms to exhibit significant differences in their use of limiting resources (Chesson 2000; MacArthur 1972; Tilman 1976, 1980, 1982). Specifically, three conditions are necessary for stable coexistence in resource competition models [and Chase & Leibold's (2003) extension to CNT]. There must be ecological trade-offs that cause (a) the ZNGIs of competitors to intersect and (b) species to consume more of the resource that most limits their growth (as indicated by the slope of the consumption vector), and (c) the environment's supply point must lie between the consumption vectors describing the impact niche. For any two niche axes and a given supply point, only two species may stably coexist, but variability in supply points across space or the addition of new niche axes produce more ways to coexist (Chase & Leibold 2003, Tilman 1982). Although it is true that most plant roots take up a limited number of inorganic nutrients (NH₄, NO₃, PO₄), the diversity of organic forms that ectomycorrhizal fungi access (see Section 2) could increase the diversity of soil resource axes and therefore the potential for coexistence.

Mycorrhizal-based niche partitioning should require some degree of specialization, so that plants either interact strongly with different fungal partners or exchange resources at different rates. This is most likely to be true for competition among arbuscular mycorrhizal, ectomycorrhizal,

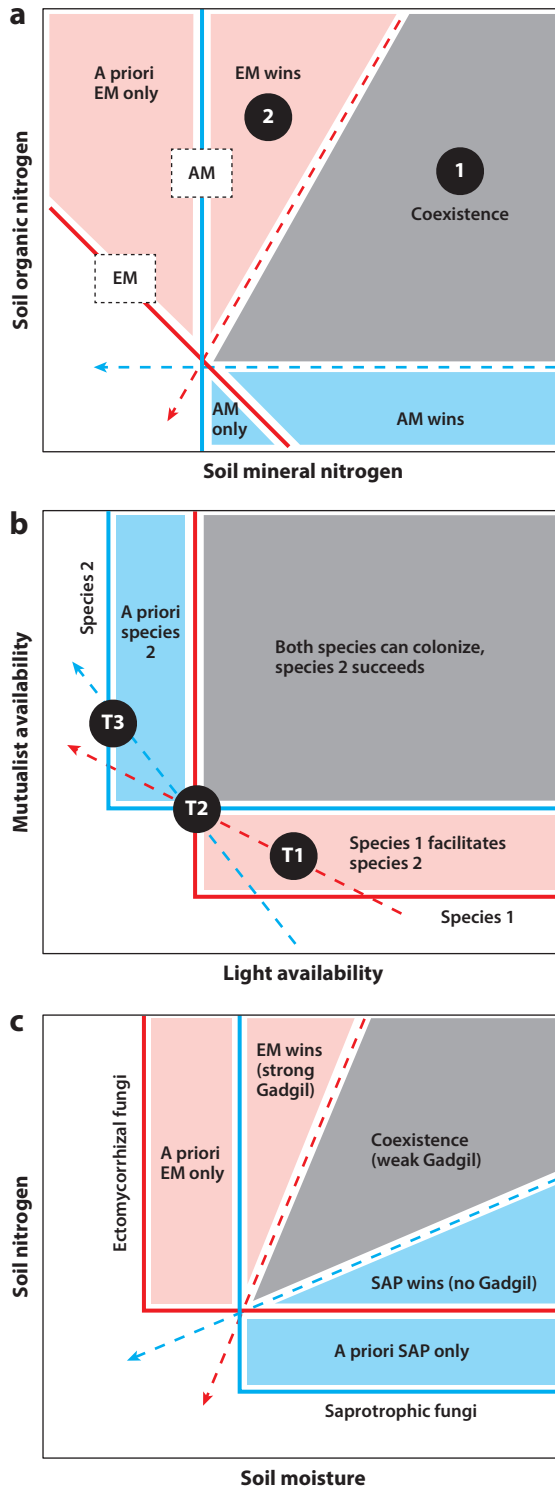
and ericoid mycorrhizal plants. Although arbuscular mycorrhizal and ectomycorrhizal fungi are sometimes contrasted as phosphorus and nitrogen specialists, respectively, little evidence that ectomycorrhizal fungi are poor competitors for phosphorus has been found (Finlay 1989). Rather, one of the biggest functional distinctions between these three forms of mycorrhizal symbioses seems to be an increasing ability to liberate and take up nitrogen and phosphorus directly from organic sources (Read 1991), with the general pattern being arbuscular mycorrhizal < ectomycorrhizal < ericoid mycorrhizal fungi. Even though evidence that plant coexistence may be facilitated via specialization on different N-forms has been found (McKane et al. 2002), to my knowledge no empirical tests of how resource partitioning influences competition among plants with different forms of mycorrhizal symbiosis have been performed (but see Steidinger et al. 2014 for an empirical test of resource partitioning), despite the fact that the idea has been in the literature for some time (Aerts 2002, Bever et al. 2010, van der Heijden 2002). There are notable situations in which a particular ectomycorrhizal plant species may also host arbuscular (Dickie et al. 2001) or ericoid mycorrhizal fungi (Vralstad et al. 2002), and future work should also explore the consequences of limited partner overlap on coexistence.

In **Figure 2a** I use the CNT model to present what I think is the most biologically plausible hypothesis for competition between arbuscular mycorrhizal mutualists, which specialize on inorganic nitrogen, and ectomycorrhizal mutualists, which can take up both inorganic and organic forms of nitrogen. One assumption of this model is that acquisition of organic nitrogen through ectomycorrhizal symbiosis involves some trade-off. This assumption seems plausible, given both the cost to produce extracellular enzymes for organic nitrogen acquisition (Lindahl & Tunlid 2015, Talbot et al. 2015) and the greater fraction of net primary productivity ectomycorrhizal fungi receive (~7–30%), as compared with arbuscular mycorrhizal fungi (~2–20%) (Leake et al. 2004).

Two important outcomes of this model are (a) that for the two types of symbiosis to coexist, ectomycorrhizal symbionts must prefer and consume organic over inorganic nitrogen and (b) coexistence is possible only when the supply of inorganic nitrogen is relatively high. A direct corollary of these results is that ectomycorrhizal plants and fungi should exclude arbuscular

Figure 2

Mycorrhizal symbiosis and community dynamics. (a) Resource competition between arbuscular mycorrhizal (AM) plants specializing in inorganic nitrogen and ectomycorrhizal (EM) plants able to use both inorganic and organic nitrogen. Zero net growth isoclines (ZNGIs) and impact vectors are depicted by solid and dashed lines, respectively. At supply points falling between the two impact vectors (e.g., supply point 1, in the *gray area*), coexistence is possible. However, for supply points in shaded regions outside the impact vectors, either arbuscular (*blue*) or ectomycorrhizal (*red*) symbiosis is predicted to dominate competition. Only one species can occur a priori if the supply point falls outside of the other species' requirement niche. Predominance of organic nitrogen (supply point 2) is linked to phenomena such as tropical monodominance and the increase in ectomycorrhizal associations at high latitude and high elevation. (b) Predicting successional dynamics using a shared mutualist as a niche axis. Plants increase (rather than reduce) mutualist availability, which can be depicted as a positive impact vector. Here we show a temporal sequence in which a plant with low mycorrhizal dependence may colonize when mycorrhizal fungi are rare (T1). Over time mutualist abundance is increased to a point (T2) at which a second, more shade-tolerant species can colonize. The second species eventually wins because it reduces light availability and can maintain population growth at a lower level of light than the first species (T3). (c) Competition between mycorrhizal fungi and saprotrophs (SAP) is thought to reduce decomposition rates and increase carbon storage (Gadgil effect). If mycorrhizal fungi are more limited by nitrogen and saprotrophs are more limited by water, then the strength of the Gadgil effect will change along a moisture gradient. This model makes the testable prediction that equilibrium soil nitrogen and moisture will be at intermediate levels (the ZNGIs intersection point) when both groups are present.



mycorrhizal plants and fungi when organic nitrogen supply is high relative to inorganic, and they should be excluded when it is low. Surprisingly, this relatively simple model underlies a number of other predictions about the edaphic and biogeographic distribution of mycorrhizal symbiosis (Section 3.3). The same model could be easily extended to model competition between other types of mycorrhizal associations (e.g., Aerts 2002), and supportive evidence that in heathlands nitrogen fertilization leads to an increase in arbuscular versus ericoid mycorrhizal plants has been found (Heil & Diemont 1983).

Although the greatest potential for both host specialization and functional differentiation exists broadly across arbuscular mycorrhizal, ectomycorrhizal, and ericoid mycorrhizal symbioses, evidence that mycorrhizal resource partitioning could occur between plants with the same mycorrhizal association type has also been found. Local mycorrhizal communities generally contain dozens (arbuscular and ericoid mycorrhizal) to hundreds (ectomycorrhizal) of fungal species, and field studies of co-occurring plant species of the same mycorrhizal association type have typically shown large overlap among the mycorrhizal fungi species that colonized the plant roots (Opik et al. 2009, Peay et al. 2015, Toju et al. 2013), suggesting that host generalism is the rule. Nonetheless, some evidence of strict specificity (e.g., the ectomycorrhizal suilloid fungi and Pinaceae) (Bruns et al. 2002) and preference (i.e., quantitative differences in association) (Ishida et al. 2007, Tedersoo et al. 2010) within a mycorrhizal association type has been found. When plant species vary in their growth response to the same mycorrhizal fungal species (Bever 2002, Hoeksema et al. 2009, Klironomos 2003), the presence of that fungus can alter competitive outcomes (van der Heijden 2002, Wagg et al. 2011). Van der Heijden et al. (1998) found that experimentally increasing the richness of arbuscular mycorrhizal fungi in plant mesocosms increased plant species richness, total nitrogen uptake, and productivity; this finding is consistent with the theory that mycorrhizal fungi reduce plant niche overlap. Thus, there are reasons to believe that mycorrhizal fungi could promote plant coexistence through resource partitioning, but more empirical studies are needed to link specificity and functional differentiation to coexistence using a framework similar to **Figure 2a**, particularly for ectomycorrhizal symbioses.

Coexistence through resource partitioning is well suited to the mutualistic niche concept presented here, but mycorrhizal fungi may promote plant coexistence by a number of other mechanisms. For example, Bever (2002) has shown that when plants cultivate mycorrhizal fungi that are less beneficial to themselves than to other plant species, negative density-dependent feedbacks can develop that prevent competitive dominance in a manner similar to those developed by host-specific pathogens (Janzen 1970). Alternatively, the commonly observed overlap in mycorrhizal fungi between co-occurring plant species could lead to functional convergence in resource uptake, rather than differentiation. If convergence in resource uptake serves to reduce competitive differences between species, it could act as an equalizing mechanism (sensu Chesson 2000) that prevents competitive exclusion (although long-term coexistence would still require some niche differences). Such equalizing effects could also result from common mycorrhizal networks, in other words, multiple plants physically linked through the same mycorrhizal fungal individual. Sink-source dynamics may lead to net resource transfer from dominant to inferior competitors (Simard et al. 1998), although the ecological relevance of these transfers is a matter of some debate (Robinson & Fitter 1999).

3.2. Mycorrhizas and Local Competitive Advantage

Figure 2a also suggests conditions under which mycorrhizal symbiosis could lead to competitive dominance. Perhaps one of the most-studied examples of mycorrhizal-based competitive exclusion is the case of tropical forest monodominance. Most tropical rainforests are highly diverse, with even

the most common species making up <10% of total biomass or individuals, but there are striking examples of tropical forest stands dominated by a single species (Torti et al. 2001). Although most tropical tree species are arbuscular mycorrhizal (Brundrett 2009, McGuire et al. 2008), a striking number of the species that can form monodominant stands are ectomycorrhizal (Torti et al. 2001), and experimental evidence suggests that the presence of the ectomycorrhizal fungi is necessary for monodominance (McGuire 2007). One of the leading explanations is that ectomycorrhizal-mediated monodominance occurs when the local nutrient economy is dominated by organic nitrogen that is accessible only to trees with ectomycorrhizal fungi (i.e., moving from supply point 1 to supply point 2 in **Figure 2a**). Consistent with this explanation, the presence of ectomycorrhizal associations was strongly correlated with spatial patterns of decreased nitrogen mineralization within a tropical dry forest in Costa Rica (Waring et al. 2016). Corrales et al. (2016) evaluated a number of hypotheses and also found that decreased mineral nitrogen supply was the most likely explanation for monodominance of the ectomycorrhizal tree *Oreomunnea mexicana* in Panama.

The case of tropical monodominance not only provides support for the general model depicted in **Figure 2a** but also raises an important question of how mycorrhizal symbiosis or other factors come to modify local nutrient economies (Phillips et al. 2013). The earliest explanations for ectomycorrhizal monodominance invoked poor-quality plant litter with a high C:N ratio that exacerbated nutrient limitation in the poor soils where these stands are often found (Connell & Lowman 1989). This explanation is consistent with the resource ratio model in **Figure 2a**, as a high C:N ratio in litter and soil tends to be associated with decreased nitrogen mineralization rates and thus an increased ratio of organic-to-mineral nitrogen forms in soil (Parton et al. 2007). However, tissue C:N ratios do not vary consistently among ectomycorrhizal and arbuscular mycorrhizal tree species, particularly once phylogeny has been accounted for (Koele et al. 2014). Thus, Dickie et al. (2014) have recently argued that ectomycorrhizal fungi can directly alter the decomposition process independent of litter chemistry. Indeed, ecosystem models that incorporate direct organic nitrogen uptake by ectomycorrhizal fungi, as depicted by the consumption vector in **Figure 2a**, find that the increased competition for nitrogen reduces saprotrophic microbial carbon consumption and can, by itself, increase soil C:N ratios (Orwin et al. 2011). The available evidence suggests that both plant litter and direct ectomycorrhizal fungal effects may contribute to shifting the local supply ratio of mineral and organic nutrient forms, as suggested for temperate forests (Phillips et al. 2013), but their relative importance may vary between systems.

One important insight from this niche-based model of resource competition is that the benefits of ectomycorrhizal fungi for plant hosts may sometimes be best understood in a community context. For example, ectomycorrhizal fungi that sometimes immobilize large amounts of soil nitrogen without passing any to their hosts (Koide & Kabir 2001, Nasholm et al. 2013) could still benefit their hosts indirectly by drawing down mineral nitrogen to a level below that needed by competing arbuscular mycorrhizal plants. A market model developed by Franklin et al. (2014) showed that an ectomycorrhizal strategy could outcompete a nonmycorrhizal strategy via this mechanism. Although the focus of their model was competition between mycorrhizal and nonmycorrhizal roots of the same tree species, the result also agrees with predictions from interspecific resource competition. These competitive benefits may help explain the evolutionary stability of mycorrhizal symbiosis despite a number of cases in which no growth benefits were observed (Hoeksema et al. 2010, Johnson et al. 2010).

3.3. Habitat Specialization and Functional Biogeography

Larger-scale spatial patterns of turnover in plant and fungal communities can also be explained by the mycorrhizal mutualistic niche model (**Figure 2a**), which predicts that ectomycorrhizal

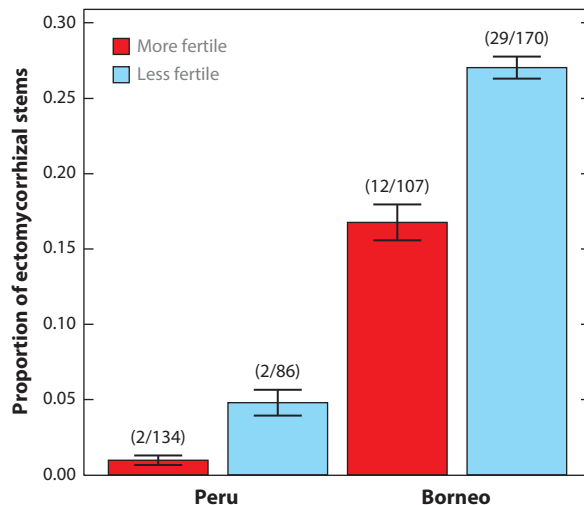


Figure 3

Biogeographic and edaphic variation in the prevalence of ectomycorrhizal symbiosis in tropical rainforests. Data come from a network of 23 (Peruvian Amazon) (Baraloto et al. 2011) and 105 (Malaysian Borneo) (Potts et al. 2002) forest inventory plots. Plots from each region were separated into relatively high-fertility (*red bars*) and low-fertility (*blue bars*) soils: White-Sand versus Terre Firme (Peru) and Udult versus Humult (Borneo). Numbers in parentheses represent the average number of ectomycorrhizal tree species and the total number of tree species for plots in each soil type.

symbiosis should be most common where inorganic nitrogen supply is low relative to organic nitrogen supply. Both local and large-scale patterns in ectomycorrhizal symbiosis appear to follow this prediction, increasing in prevalence in both colder climates (with latitude and elevation) (Dickie et al. 2014, Read 1991) and infertile soils. For example, in tropical rainforests in Borneo and Peru the proportion of ectomycorrhizal trees increases from relatively fertile clay soils to infertile sandy soils (**Figure 3**). Although ectomycorrhizal trees tend to be relatively rare in lowland neotropical rainforests (outside of monodominant stands), neotropical montane forests are characterized by ectomycorrhizal plant genera such as *Quercus*, *Alnus*, and *Oreomunnea*. Similarly, temperate and boreal forests are dominated by ectomycorrhizal tree genera, such as *Pinus*, *Picea*, and *Quercus* in the northern hemisphere and *Eucalyptus* or *Nothofagus* (*sensu lato*) in the southern hemisphere, in which nitrogen is the primary limiting nutrient to plant growth and organic forms of nitrogen are more abundant (Read 1991).

Although these patterns of functional biogeography seem to fit a niche model, ectomycorrhizal abundance may also be influenced by other factors not directly related to the niche. For example, neotropical and paleotropical forests with largely similar climate and soils exhibit historical differences in species composition that influence their functional biogeography. In Borneo, ectomycorrhizal trees make up > 10 times the proportion of individuals (22%) than in the Peruvian Amazon (2%) (**Figure 3**). Similarly, Dickie et al. (2013) found inconsistent patterns in plant mycorrhizal association type when examining vegetation change along developmental chronosequences during which nutrients become progressively limiting. Some of this compositional variability likely results from strong priority effects leading to historical contingency during community assembly (Fukami 2015), which could override the advantages of particular mycorrhizal types with respect to local nutrient conditions. In addition, although I have focused on the functional benefits of

being ectomycorrhizal in competing for organic nitrogen, some local species pools may contain other plant strategies that compete well for organic nutrients, such as cluster roots (Steidinger et al. 2014). Thus, the final state of a given system is not strictly dependent on mycorrhizal niche factors but also depends on historical factors that shape community assembly and the functional traits of the local species pool.

3.4. The Mutualistic Regeneration Niche

Despite their importance in expanding niche space for plants and fungi, mycorrhizal symbioses are not vertically transmitted. Each new generation of partners must find each other in the environment. The idea that microbes are dispersal unlimited (i.e., everything is everywhere) made it plausible to ignore microbial community dynamics in plant ecology. It has recently become clear, however, that limited dispersal contributes to spatial heterogeneity in fungal community composition (Peay & Bruns 2014, Peay et al. 2010). This spatial heterogeneity is due in part to strong priority effects during mycorrhizal fungal competition (Kennedy 2010, Werner & Kiers 2015), which generate historical contingency in community assembly when there is variability in the order species disperse to a new site (Fukami 2015). The effect of limited long-range dispersal is also evident in the strong biogeographic patterns recently detected for ectomycorrhizal and other fungi (Talbot et al. 2014, Tedersoo et al. 2014). At the local scale, plants recruiting near either conspecifics or other compatible ectomycorrhizal hosts are rapidly colonized by vegetative mycelium from established plants (Nara & Hogetsu 2004), but seeds that fall outside of existing root zones require mycorrhization via spores or other dispersal propagules (e.g., sclerotia). Although fungal spore production is prolific, reaching trillions per km² for individual species, quantities decrease exponentially away from spore sources (Peay et al. 2012). As a result, ectomycorrhizal establishment and diversity on seedlings begins to decline anywhere from 10s to 1,000s of meters from established ectomycorrhizal vegetation (Dickie & Reich 2005, Peay et al. 2012).

The challenges of finding a plant host are evident in the reproductive investment and variety of dispersal strategies observed in ectomycorrhizal fungi. Dispersal traits—such as relative investment in fruiting bodies, dispersal vector, and production of stress-resistant or dormant spores—can predict spatial and temporal patterns in ectomycorrhizal community structure (Bruns et al. 2009; Peay et al. 2007, 2012). Dispersal traits are also correlated with other traits that may represent life history syndromes. For instance, some of the best dispersers are also highly host specific (Hayward et al. 2015), and evidence for a dispersal–competition trade-off has been found (Kennedy et al. 2011). The implications of such spatial and temporal variability of local ectomycorrhizal fungal inoculum due to dispersal limitation and differences in dispersal traits can be explored using a niche model.

In a host plant niche model, each fungal mutualist may be treated as a niche axis of inoculum abundance (**Figure 2b**). As a result, plants with low ectomycorrhizal requirement niches (or which associate with host specialists that are effective dispersers, such as the pine–suilloid relationship (Hayward et al. 2015, Peay et al. 2012) may facilitate other plants by increasing inoculum levels or recruiting generalist fungi after they establish. **Figure 2b** illustrates a hypothetical plant succession using the niche model. The system starts at the supply point indicated by T1, at which mycorrhizal inoculum that both species can use is too low for species 2 to sustain a population. However, plant species 1 can establish first and increase the availability of mycorrhizal inoculum to a point at which plant species 2 can colonize (T1 to T2, **Figure 2b**). Species 2 then reduces light levels (T2 to T3, **Figure 2b**), which excludes species 1. Although the mechanics of this particular model have not been specifically tested, good examples exist of mycorrhizal facilitation of late successional hosts by early successional hosts (Horton et al. 1999).

3.5. The Mycorrhizal Niche and Fungal Coexistence

Only recently have fungal competition and coexistence received attention from ecologists. Recent molecular studies indicate that the local species pool of ectomycorrhizal fungi for a given forest type is minimally in the range of 100–300 species (Ishida et al. 2007, Peay et al. 2015, Taylor et al. 2014). Lower-diversity communities have been described in some tropical forests (Tedersoo et al. 2010) and plant invasions (Hayward et al. 2015) but are less common. Anderson et al. (2014) examined the fine-scale distribution of ectomycorrhizal roots and fungal hyphae in 2-cm³ soil cubes and detected an average of 2–4 species of ectomycorrhizal fungi co-occurring, with a maximum of 11 species. This observation agrees with other studies of ectomycorrhizal fungal diversity on host roots and as hyphae in single-soil cores (Peay et al. 2010). Gene mapping studies show that ectomycorrhizal fungal individuals commonly extend over 1–10 m of the forest floor (Redecker et al. 2001), so co-occurrence at the centimeter scale indicates ample opportunity for interactions. In addition, soil is perhaps the highest-diversity habitat on Earth, and ectomycorrhizal fungi routinely coexist with hundreds of species of bacteria and saprotrophic fungi, as well as invertebrate animals (nematodes, collembola, mites) and protozoans at the centimeter scale. Such high levels of diversity demand explanation, and how ectomycorrhizal mutualism affects the fungal niche strongly affects diversity and function of soil microbial communities.

Direct access to plant metabolites has changed the impact niche of ectomycorrhizal fungi, which in theory could increase their ability to coexist with saprotrophs by reducing competition for soil carbon. By contrast, competition between the two guilds could be intense for shared limiting resources like nitrogen. Thus, recent interest in competition between the two guilds is driven by its potential consequences on ecosystem nutrient cycling. For example, a global survey of forest soils by Averill et al. (2014) concluded that competition between ectomycorrhizal fungi and saprotrophs increases carbon storage relative to forest ecosystems dominated by arbuscular mycorrhizal associations. Early research by Gadgil & Gadgil (1971) showed that trenching to exclude ectomycorrhizal fungi resulted in competitive release of saprotrophs, as evidenced by increases in decomposition activity that led to decreases in standing leaf litter after 12 months. Many of the explanations for the potential of ectomycorrhizal fungi to increase ecosystem carbon storage involve mycorrhizal–saprotroph competition for shared limiting resources, such as nitrogen and water (Fernandez & Kennedy 2015, Gadgil & Gadgil 1971). Koide & Wu (2003) found that the ability of ectomycorrhizal fungi to limit saprotrophs depended on soil moisture concentration. This idea can be translated into the graphical niche framework by assuming that ectomycorrhizal fungi require more nitrogen and that saprotrophic fungi require more moisture (**Figure 2e**). Logically, mycorrhizal fungi should require more nitrogen as they must meet both their own and their host's needs. In addition, some evidence suggests that ectomycorrhizal fungi can acquire water from their hosts during extreme drought via hydraulic redistribution (Querejeta et al. 2003). The niche model predicts both the context-dependent effect of soil moisture supply on competition, consistent with Koide & Wu (2003), and the lack of evidence for Gadgil effects in wet tropical climates (Fernandez & Kennedy 2015). Interestingly, the niche model also predicts that competition between the two fungal guilds will cause total soil nitrogen and water content to reach concentrations intermediate to those reached when only one guild is present.

Although ectomycorrhizal fungi no longer use or require soil organic carbon, all ectomycorrhizal fungi compete with each other for carbon from plant roots, and evidence shows that competition for this resource can be intense and lead to total exclusion of some ectomycorrhizal fungal species (Kennedy 2010, Mujic et al. 2016). Nevertheless, molecular studies have shown community differentiation along a number of key environmental niche axes, such as gradients of carbon, nitrogen, phosphorus, base cations, organic matter, soil moisture, and pH, and such

differentiation could contribute to coexistence (e.g., Dickie et al. 2002). In addition, ample evidence exists for functional specialization of ectomycorrhizal fungi on different soil resources on the basis of differential production of enzymes and genomic content (Courty et al. 2005, Kohler et al. 2015). Even though these observations suggest that niche mechanisms contribute to coexistence of ectomycorrhizal fungi, most of the data are correlational in nature. Experiments using the resource competition (Tilman 1982) and CNT frameworks (Chase & Leibold 2003) would be excellent ways to identify the niche axes and key functional trade-offs that contribute most to coexistence.

Perhaps the most unusual aspect of within-guild competition arises from the fact that carbon allocation by the host tree may help determine fungal winners and losers. Host plants can differentially allocate carbon to arbuscular mycorrhizal partners, even when they are not spatially segregated among roots (Kiers et al. 2011). Convincing models for fine-scale plant control of carbon flow to ectomycorrhizal fungi include regulation of apoplastic sucrose transport, invertase production, and hexose uptake (Nehls et al. 2007). If plant carbon allocation is linked to resource exchange, however, it should lead to exclusion of inferior mutualists that provide fewer benefits. Given the high local diversity of ectomycorrhizal fungal communities, plant-control models suggest either that the plant must receive and value different benefits from ectomycorrhizal fungal species or that mechanisms exist to maintain inferior partners.

Biological market models have proven useful for understanding how hosts maximize benefits when trading resources and how this might impact local coexistence of ectomycorrhizal fungi (Schwartz & Hoeksema 1998). Using one such model, Kummel & Salant (2006) showed that a plant generally switches to the mycorrhizal fungus with the lowest per unit resource cost and that multiple partners will persist only when the fungi have different (convex and concave or linear) resource exchange functions. More recently, Moeller & Neubert (2016) used optimal control theory to show that, in variable environments, plants can maximize growth by actively maintaining mycorrhizal fungi that are currently competitively inferior (i.e., those that are more expensive). Even though this model requires empirical tests, strong seasonal changes in soil environment (and microbial communities) (Voriskova et al. 2014) coupled with the notable intra-annual fluctuation in ectomycorrhizal fungal species abundances (Koide et al. 2007) make this mutualistic storage effect a plausible mechanism for maintaining local mycorrhizal fungal species diversity. Although these theoretical models provide an important starting point, empirical work is necessary to validate their predictions and determine the extent to which plants can differentially allocate resources to different fungi.

4. EVOLUTIONARY CONSIDERATIONS OF THE MUTUALISTIC NICHE

Although it seems clear that mutualism has expanded the niches of both plant and fungal participants, it may also have led to loss or reduction of autonomous function and performance—in other words, contraction of the individualistic niche over evolutionary time. This contraction is particularly apparent on the fungal side, and recent analyses have shown repeated loss of genes and/or reduction in the production of enzymes associated with carbohydrate acquisition across multiple independent ectomycorrhizal fungal lineages (Kohler et al. 2015, Talbot et al. 2015). Although some ectomycorrhizal fungi can be cultivated axenically, unlike their close saprotrophic relatives they are never found free-living in nature, and their plant hosts are also rarely uncolonized by fungi in natural settings. Less evidence for gene loss on the plant side has been found, but pines appear to lack the ancestral genes for arbuscular mycorrhizal symbiosis (Garcia et al.

2015). Further, most ectomycorrhizal plants grow very poorly in the absence of their fungal partners unless heavily fertilized (Smith & Read 2008), and although variation in ectomycorrhizal dependence certainly exists (Pryor 1956, Vozzo & Hacsakaylo 1974), even highly dependent plants may persist for a short time without fungal partners (Collier & Bidartondo 2009). In this sense, ectomycorrhizal plants and fungi provide both a good and a bad example of the importance of the mutualistic niche concept, as the individualistic niche may only exist now in highly artificial conditions. Despite the reduction of autonomous function, ectomycorrhizal associations appear to be stable over evolutionary time (Bruns & Shefferson 2004).

5. CONCLUSION

What is gained by explicitly including mutualism into the niche concept? First, it makes our concept of the niche a more accurate reflection of the biological world. Although there has been debate about the prevalence of competition in ecology, the existence of mutualisms is inescapable. A lone plant on a rocky slope may not be competing with other plants, but its fitness almost certainly depends on its ability to engage mycorrhizal mutualists or attract pollinators. This reality should be explicitly integrated into ecological thinking and teaching. Second, explicitly incorporating mutualism into a niche framework identifies important ecological research opportunities. Few mutualistic niches have been mapped, and there is room for progress in identifying appropriate niche axes, identifying important functional trade-offs, measuring the impact of mutualism on coexistence, and determining the appropriate theoretical framework for this endeavor. As a starting point, I have proposed some models based on CNT. Other models may provide additional insights, but the CNT models I have used should easily extend to other forms of mutualisms. For example, legume–rhizobia mutualisms should have strong impacts on nutrient supply points. The effects of endophytic fungi on host plant physiology could be included using a niche axis for heat or drought stress (Afkhami et al. 2014, Marquez et al. 2007). Similarly, axes quantifying mutualist abundance could be used to model competition between plants for shared pollinators (Warren et al. 2014). Third, and most important, niche models of mutualism can provide unifying explanations for outstanding ecological questions. For example, a mutualistic niche framework may explain why some mutualisms are widespread and stable despite the fact that cooperation does not always provide clear growth benefits. Similarly, by accounting for the influence of biotic and abiotic factors on resource supply points, this simple graphical niche model can potentially explain a variety of ecological patterns, such as tropical monodominance, edaphic habitat specialization, and latitudinal gradients of mycorrhizal mutualism. Finally, explicitly recognizing how mutualisms impact species' niches has practical applications. For instance, the ability of a species to shift its range as climate changes will depend on whether its mutualist is already available in the new zone or can migrate there (Rusca et al. 2006, Lankau & Keymer 2016), factors that could depend critically on the mutualist's niche. Further, climate changes alter plant communities, and concomitant changes in identity or population density of mycorrhizal mutualists may alter patterns of carbon storage and nutrient cycling. Niche models that incorporate mutualism can help predict these patterns and help us to understand how species can transcend the limits of their own genes.

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Contents

The Phyllosphere: Microbial Jungle at the Plant–Climate Interface <i>Corinne Vacher, Arndt Hampe, Annabel J. Porté, Ursula Sauer, Stéphane Compant, and Cindy E. Morris</i>	1
An Evolutionary Genetic Perspective on Cancer Biology <i>Max Shpak and Jie Lu</i>	25
Is There a Genetic Paradox of Biological Invasion? <i>Arnaud Estoup, Virginie Ravigné, Ruth Hufbauer, Renaud Vitalis, Mathieu Gautier, and Benoit Facon</i>	51
Evolutionary History, Selective Sweeps, and Deleterious Variation in the Dog <i>Adam H. Freedman, Kirk E. Lohmueller, and Robert K. Wayne</i>	73
Forests, Climate, and Public Policy: A 500-Year Interdisciplinary Odyssey <i>Gordon B. Bonan</i>	97
Evolution and Extinction of Land Snails on Oceanic Islands <i>Satoshi Chiba and Robert H. Cowie</i>	123
The Mutualistic Niche: Mycorrhizal Symbiosis and Community Dynamics <i>Kabir G. Peay</i>	143
A Genomic Perspective on the Generation and Maintenance of Genetic Diversity in Herbivorous Insects <i>Andrew D. Gloss, Simon C. Groen, and Noah K. Whiteman</i>	165
Integrating Paleontological and Phylogenetic Approaches to Macroevolution <i>Gene Hunt and Graham Slater</i>	189
Structure and Functioning of Dryland Ecosystems in a Changing World <i>Fernando T. Maestre, David J. Eldridge, Santiago Soliveres, Sonia Kéfi, Manuel Delgado-Baquerizo, Matthew A. Bowker, Pablo García-Palacios, Juan Gaitán, Antonio Gallardo, Roberto Lázaro, and Miguel Berdugo</i>	215
The Evolutionary Ecology of Animals Inhabiting Hydrogen Sulfide–Rich Environments <i>Michael Tobler, Courtney N. Passow, Ryan Greenway, Joanna L. Kelley, and Jennifer H. Shaw</i>	239

The Mechanisms and Consequences of Interspecific Competition Among Plants <i>Erik T. Aschehoug, Rob Brooker, Daniel Z. Atwater, John L. Maron, and Ragan M. Callaway</i>	263
Infectious Disease Dynamics in Heterogenous Landscapes <i>Steven R. Parratt, Elina Numminen, and Anna-Liisa Laine</i>	283
Evolution and Ecology of CRISPR <i>Edze R. Westra, Andrea J. Dowling, Jenny M. Broniewski, and Stineke van Houte</i> ...	307
Patterns, Causes, and Consequences of Anthropocene Defaunation <i>Hillary S. Young, Douglas J. McCauley, Mauro Galetti, and Rodolfo Dirzo</i>	333
Coexistence in Close Relatives: Beyond Competition and Reproductive Isolation in Sister Taxa <i>Marjorie G. Weber and Sharon Y. Strauss</i>	359
Mediterranean Biomes: Evolution of Their Vegetation, Floras, and Climate <i>Philip W. Rundel, Mary T.K. Arroyo, Richard M. Cowling, Jon E. Keeley, Byron B. Lamont, and Pablo Vargas</i>	383
Characterizing Species Interactions to Understand Press Perturbations: What Is the Community Matrix? <i>Mark Novak, Justin D. Yeakel, Andrew E. Noble, Daniel F. Doak, Mark Emmerson, James A. Estes, Ute Jacob, M. Timothy Tinker, and J. Timothy Wootton</i>	409
Evolutionary Legacy Effects on Ecosystems: Biogeographic Origins, Plant Traits, and Implications for Management in the Era of Global Change <i>Jeannine Cavender-Bares, David D. Ackerly, Sarah E. Hobbie, and Philip A. Townsend</i>	433
Modularity: Genes, Development, and Evolution <i>Diogo Melo, Arthur Porto, James M. Cheverud, and Gabriel Marroig</i>	463
The Role of Symbiotic Microbes in Insect Invasions <i>Min Lu, Jiri Hulcr, and Jianghua Sun</i>	487
Ecological Opportunity and Adaptive Radiation <i>James T. Stroud and Jonathan B. Losos</i>	507
Indexes	
Cumulative Index of Contributing Authors, Volumes 43–47	533
Cumulative Index of Article Titles, Volumes 43–47	537

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://www.annualreviews.org/errata/ecolsys>