CHAPTER 19

The biogeography of ectomycorrhizal fungi – a history of life in the subterranean

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19.1 Why study the biogeography of ectomycorrhizal fungi?

The science of biogeography maps spatial patterns of biological diversity as a means of understanding the evolutionary and ecological processes that structure life on this planet (Lomolino *et al*., 2006). Understanding spatial patterns of biodiversity has given rise to some of the most important discoveries in modern science. The unique composition of flora and fauna in different parts of the world, coupled with the spatial and temporal coincidence of allied species, led both Darwin and Wallace to the idea of evolution by natural selection (Darwin, 1859; Wallace, 1855). Similarly, Wegener's theory of continental drift was formulated in great part by the realization that the fossil record provided a window into the past arrangement of landmasses, precisely because of the spatially restricted nature of species distributions. Biogeography may not be a field familiar to most lay people or most microbiologists, but it is a powerful window into life on this planet.

The documentation of basic biogeographic patterns is fundamental to understanding any taxonomic group. Knowing the time or place that an organism first arose and diversified provides a window into the ecological and evolutionary processes shaping their diversity and tells us how they responded to past changes in the environment, or how they might fare under new climates. Yet, for the organisms studied by microbiologists (fungi, bacteria, viruses) and that constitute the majority of life on earth, basic details of biogeography remain poorly known, and are still a subject of debate.

Biogeography was one of the earliest branches of plant and animal biology, but the development of microbial biogeography lagged, because the use of morphological systematics to differentiate microbes and reconstruct their evolutionary histories was a "fruitless search", to quote Carl Woese (Woese, 1987). As a result of the paucity of morphological characters, until very recently many microbes were thought to lack distinct biogeographical patterns (Finlay, 2002; Peay *et al*., 2010c), and the importance of these organisms to the diversity and function

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of earth systems was underappreciated (Falkowski *et al.*, 2008). The molecular revolution in DNA sequencing (Horton and Bruns, 2001; Woese, 1987) has provided the tools necessary for accurate identification and mapping of microbial distributions, and is forcing reevaluation of microbial biogeography.

Ectomycorrhizal fungi (EMF) are obligate symbionts of dominant tree species in both temperate and tropical biomes, and are an important part of the diversity of terrestrial ecosystems. While ecological studies of EMF have traditionally focused on local-scale processes, understanding the large-scale distributional patterns of these organisms can shed light onto many key biological questions, such as the role of symbiosis in shaping species distributions, and how nutrient mutualisms are affected by climate and geology. Mushroom-forming fungi are relatively rich in morphological features among microbial groups. However, the study of their biogeography has also progressed slowly.

In this chapter, we review the current state of EMF biogeography in light of new data stemming from the use of DNA-based molecular tools. We begin first with a look at the pre-molecular history of EMF biogeography, before turning to recent developments. The remainder of the review moves from smaller to longer temporal scales, beginning with current species' distributional patterns, and their effects on community composition and diversity at large scales. From there, we take a phylogeographic approach to examine the population level processes that give rise to species distributions over thousands of years, before finally turning to historical biogeography to examine how the movement of continents and long-distance dispersal have shaped modern distributions of EMF taxa.

19.2 Ectomycorrhizal biogeography in the pre-molecular era

The limitation placed on organisms in their ability to disperse is, perhaps, the primary driver of biogeographic patterns. This limitation creates a historical tie between where a species arises and its geographical distribution. Early biologists viewed fungi as organisms with incredible dispersal potential and cosmopolitan ranges. Wallace, Darwin, Candolle, and von Humboldt, upon whose writings the field of biogeography developed, were focused primarily on the distributions of plants and animals and, where fungi were noted, it was mostly to indicate their uniqueness.

Candolle, an influential Swiss botanist, alluded to this in his observation that fungi would occur, "everywhere upon the earth … when the same circumstances propitious to their production occur" (de Candolle, 1820). Similarly, the Reverend Miles Joseph Berkeley, one of the early founders of the field of mycology, wrote in a letter to Charles Darwin, "that were not Fungi so much the creatures of peculiar atmospheric conditions, there would seem to be no limit to the diffusion of their species" (Berkeley, 1863).

While Darwin and Wallace could view large-scale distributional patterns of plants and animals as a historical record of evolution precisely because of their limited ability to move between regions, the presence of fungi seems to have been seen by contemporary biologists more as a reflection of the "peculiar" environmental conditions in a particular place, rather than a record of evolutionary history. This perception was perhaps self-reinforcing; early fungal taxonomists arriving in North America expected to find European species and, as a result, (incorrectly) applied European names to the species they found – a problem that is still being sorted out today. Consequently, making biogeographic conclusions from distribution records based on morphological taxonomy can be highly misleading (Pringle and Vellinga, 2006).

The early view that fungi were "unreliable as biogeographic markers", coupled with a paucity of reliable taxonomic data, slowed the development of fungal biogeography (Pirozynski, 1983) for nearly a century. However, improved fungal taxonomy and increased global migration of European or North American trained systematists led to some attempts to assemble geographic distribution information for fungi, and to determine the extent to which factors such as climate or host identity affected these distributions (Bisby, 1943). Pirozynski (1983) was an early champion for the study of EMF as a window into biogeography, as he suspected that their tight associations with host plants would more greatly limit their dispersal and lead to distinct geographic patterning, compared with other fungal groups. Still, he suspected much less endemism in fungi than in plants, at least in the context of insular islands.

Biogeographic hypotheses began to emerge, particularly for distinct groups with clear centers of diversity. For example, the strongly southern hemisphere-biased distribution for the genus *Rozites* was thought to suggest a Gondwanan origin (Bougher *et al.*, 1994; Horak, 1981). However, distinguishing amongst finer-scale biogeographic scenarios was difficult. In examination of some Central American *Rozites*, for example, Halling (Halling and Ovrebo, 1987) noted that it was not possible to tell if they were northern co-migrants with oaks from an Indo-Malayan land bridge, or had migrated north from South American Nothofagaceae (southern beech) associates. In hindsight, however, none of these scenarios is likely correct, as these investigators were misled at a more fundamental level by the fact that the key morphological feature distinguishing *Rozites* as a genus (presence of a membranous veil) evolved multiple times independently in the Cortinariaceae (Peintner *et al.*, 2002).

Even for more conspicuous taxa, basic biogeographic patterns were difficult to distinguish. For example, Watling proposed a boreal origin for boletes (Watling, 2001), rather than an origin centered on their current day diversity in Southeast Asia (Corner, 1972). While these hypotheses were not directly testable at the time, these early scientists outlined the key questions that continue to drive the field:

(i) What are the centers of ectomycorrhizal endemism?
(ii) How important is long-distance dispersal in shaping species distributions?
(iii) What are the key migration routes that link regions?
(iv) When did this migration occur?

These questions have proved fertile grounds for the application of molecular tools to assess biogeographic patterns among closely related species or populations (the field of phylogeography), and more coarse global patterns at deeper taxonomic levels (the field of historical biogeography).

19.3 The advance of molecular phylogeography

The development of DNA-based tools for studying fungi has provided an unambiguous way to discriminate fungal species and reconstruct evolutionary relationships

(Bruns *et al.*, 1991). From the early discovery of the polymerase chain reaction (PCR) and development of fungal specific primers (Gardes and Bruns, 1993), the accessibility of DNA sequence data has increased relentlessly. The data provided by DNA sequences have advanced development of EMF biogeography in a number of critical dimensions.

First, DNA sequence data allow a very rapid means of differentiating species. The internal transcribed spacer (ITS) regions of the nuclear ribosomal RNA genes (nrDNA) are highly variable, and can often distinguish even closely related species. The generally accepted convention is that species are delineated at approximately 97% pairwise sequence similarity, a level that corresponds well with established morphological species (Hughes *et al.*, 2009; Smith *et al.*, 2007). There are, of course, exceptions at which this level of cutoff misses important details, but it is useful enough that the ITS has served as the basis for molecular species identification, and has been selected as the official barcode locus for fungi (Kõljalg *et al.*, 2013; Schoch *et al.*, 2012).

The ability to confidently assess whether two collections belong to the same species is the basis for determining accurate distributional maps for EMF species. While morphological approaches can be highly accurate with a given site or season, their reliability becomes less certain as the time and space between collections increases. For example, by sequencing both historical and modern collections, Pringle and Vellinga (2006) were able to show that *Amanita phalloides* (the death cap) was introduced to North America, and that historical collections using this name were misidentified.

Similarly, the name *Helvella lacunosa* has been broadly applied to mushrooms across North American and Europe, based on similarities in gross morphology. However, recent sequencing of ITS and large subunit genes from western North American samples revealed monophyletic groups distinct from Europe and Eastern North America and, within the western groups, there were at least four cryptic species (Nguyen *et al.*, 2013). Notably, in this case, the use of DNA sequence data is leading formal taxonomic description. Thus, distributional data can be generated to support biogeographic research, even in advance of formal taxonomy, which is often a much slower process.

Another important implication of DNA-based study of EMF communities is that distributional data can be collected from vegetative structures growing in soil. Many species fruit infrequently (Straatsma *et al.*, 2001) and may be difficult to find, particularly for species that grow in remote sites, not easily visited on a regular basis. For example, Peay *et al.* (2010b) were able to identify > 100 species of EMF in less than five days of sampling, by sequencing colonized root tips from a lowland rainforest in Borneo while, over the same time period, < 20 species of EMF were identified from fruiting bodies (Peay, unpublished). Increasing ease of data collection and international travel has led to a much greater influx of data from countries where little data were previously available (Smith *et al.*, 2011; Tedersoo *et al.*, 2007).

19.4 Ectomycorrhizal communities in space

The documentation of broad spatial patterns of biodiversity in plant and animal life is fundamental to current understanding of ecology and evolution. The differences in species composition between North America and Europe, or between tropical Southeast Asia and South America, are indicators of the separate history of evolution in these places. Similarly, the convergence in form between regions with different evolutionary histories – for example, the Mediterranean vegetation of California and southern Europe – points toward similar ecological constraints. These differences give rise to the biogeographic realms, and similarities to the biomes used in introductory textbooks (Cain *et al.*, 2014; Lomolino *et al.*, 2006). Our understanding of EMF distributional patterns lags far behind, both in terms of the distribution of the symbiosis itself and the distribution of individual species or assemblages.

Early attempts to map the distribution of EMF symbiosis itself relied on our understanding of plant communities, as obligate host associated fungi cannot grow without their hosts. These maps showed an increase in the frequency of EMF associations in temperate and boreal forests, compared with tropical forests or grasslands (Read, 1991). While it is true that EMF associations are very common in temperate and boreal forests (e.g., Pinaceae, Fagaceae), the pattern is somewhat more complicated in tropical forests. The tropical rainforests of southeast Asia are dominated by the plant family Dipterocarpaceae, which is ectomycorrhizal, and often account for over 40% of basal area. In neotropical rainforests, ectomycorrhizal host plants are generally rare, but EMF-hosting genera, such as *Coccoloba* (Polygonaceae), *Neea* and *Guapira* (Nyctaginaceae), *Dicymbe* (Caesalpinaceae), *Aldina* (Fabaceae), and *Pakaraimea* (Dipterocarpaceae) can vary wildly in abundance – from minor components (Tedersoo *et al.*, 2010b), to forming large tracts of nearly monodominant forest (Henkel, 2003; Smith *et al.*, 2013).

While Read proposed that these patterns are driven by nitrogen availability, recent studies have called into question whether the nitrogen economy of ectomycorrhizal plants truly differs from other plants (Koele *et al.*, 2012). As such, it seems highly likely that the differences in the abundance of ectomycorrhizal plants between the neo- and paleotropics is a product of the evolutionary history of these two regions, rather than differences in environmental conditions between the two.

19.5 Dispersal limitation

Documenting the global distribution of EMF species has been impossible until very recently. The ability to perform continental or global scale sampling of EMF communities *in situ* became possible with the adaptation of DNA sequencing approaches, such as 454 Pyrosequencing (Buée *et al.*, 2009) or Illumina (Smith and Peay, 2014), to generating ITS barcode sequence data. While we are still in the early stages of analyzing these large datasets, some clear patterns are beginning to emerge.

Perhaps the clearest result is that EMF are not cosmopolitan. Evidence towards this end had been accumulating from other types of data. For example, studies of EMF from poorly studied tropical regions (Peay *et al.*, 2010b; Smith *et al.*, 2011; Tedersoo *et al.*, 2010b) generally tended to show very little sequence similarity with well-sampled European or North American studies. Similarly, Sato *et al.* (2012) matched ITS sequences from fruiting bodies in a well-characterized site in Japan to global sequences in GenBank to map species' ranges, and found that most EMF had relatively restricted ranges. Similarly, a recent attempt to create a standardized database for ITS sequences (Kõljalg *et al.*, 2013) showed that approximately 80% of molecularly defined species-level operational taxonomic units (OTUs) were restricted to a single continent. A similar meta-analytic approach combined multiple second-generation sequencing studies, and also concluded that there was limited taxon sharing between biogeographic realms (Meiser *et al.*, 2014).

However, such approaches are limited, in that they combine datasets collected using different methods, rely on the accuracy of international sequence databases that are notoriously error-plagued (Bidartondo *et al.*, 2008), and generally lack associated environmental variables. From this perspective, two recent studies have attempted to examine continental-scale fungal distribution patterns using second-generation sequencing. Talbot *et al.* (2014) sequenced hundreds of soil samples from EMF-dominated pine forests across North America. Soil samples were separated into organic and mineral horizons in order to look at community composition across large spatial gradients where environments vary, but also to contrast this with the effects of steep local environmental gradients. Tedersoo *et al.* (2014a) examined data from sites across the globe, including all continents except Antarctica. Both studies used a consistent sampling approach, molecular methodology, and included hundreds of samples. In both cases, the studies found limited taxon-sharing across study sites (see Figure 19.1).

Despite the fact that Talbot and colleagues were looking at forests dominated by the

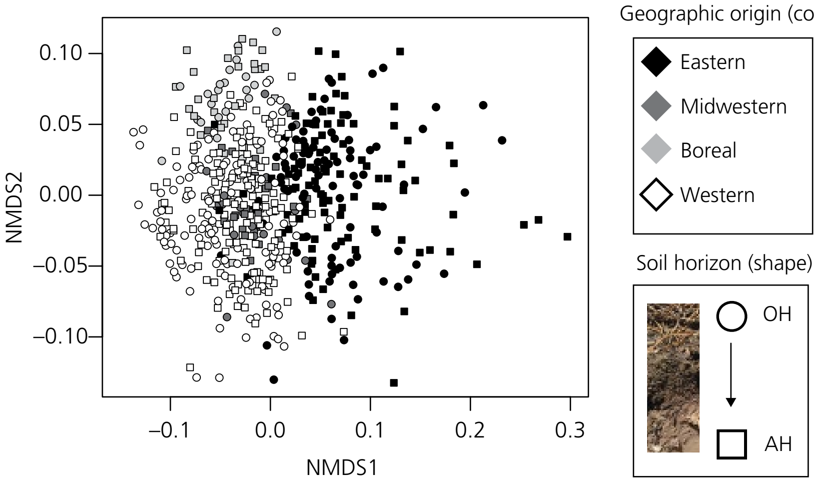

Figure 19.1 Regional differentiation of ectomycorrhizal fungal communities. The non-metric multidimensional scaling (NMDS) ordination shows community similarity of ectomycorrhizal fungi detected in 561 individual soils cores through second generation DNA sequencing of the ITS region. Soil cores were collected from essentially monodominant natural Pine stands soils across North America. Geographic location (color) and soil horizon (symbol) are mapped onto soil cores according to the legend. Ectomycorrhizal fungi communities cluster primarily by geographic locality from which they were sampled. There was little effect of soil horizon on community similarity at the continental scale, despite strong, consistent changes in soil chemistry across organic (OH) and mineral (AH) horizons. These results demonstrate that biogeographic factors are the first order determinants of ectomycorrhizal community structure. (*See insert for color representation of the figure.*)

same plant family, and that soil samples showed a very strong vertical gradient in soil chemistry, they found that EMF communities, and soil fungal communities in general, were differentiated between regions of North America, and that decay in community similarity was best predicted by distance between two samples. Tedersoo *et al.* (2014a) also found that, at a global scale, biogeographic regions contained unique species and, as a result, EMF communities clustered geographically – for example, New Guinea, Australia and New Zealand in one cluster, and Europe, West Asia, North America and East Asia in another.

While they found some evidence for taxon sharing across similar biomes, the differences between geographic regions are consistent with the effectiveness of oceans and mountains as dispersal barriers, and the historical legacy of such barriers appear to play a major role in the current structure of fungal communities. Intriguingly, a recent global study of arbuscular mycorrhizal fungi (AMF) showed very low levels of endemism and little geographic structure (Davison *et al.*, 2015). Because these two groups have a similar trophic niche, it will be important to understand whether the different patterns arise from differences in ecology (dispersal ability, host range), or evolution (clade age, evolutionary rates, taxon delineation), or both.

A major aim of these biogeographical studies is also to identify predictable drivers of EMF composition. This is particularly challenging, because factors such as climate, soil chemistry and host species composition also tend to vary at these same scales. Because it is not possible to manipulate climate or host composition at such scales, innovative approaches are necessary in order to tease apart the main drivers of these spatial effects.

One interesting approach to this is the examination of spatial patterns within a single host group. The genus *Alnus* is interesting in that it has a broad distribution (Europe, Asia, N. America, and S. America), and has a fairly unique habit, so often grows alone. A few studies have compared *Alnus* EMF communities across large scales (Kennedy *et al.*, 2011; Polme *et al.*, 2013). These studies found regional differentiation of *Alnus* EMF, and that climate and soils explain some, but not much variation. Polme found that the greatest predictor of EMF community structure was host phylogeny, even within this closely allied group of species.

Talbot *et al.* (2014) tried a similar approach, but also used the vertical soil horizon to separate spatial and environmental variables. They also found that soil chemistry explained only a small amount of variability across these large scales. Similarly, Tedersoo *et al.* (2014a) found that climate and environmental variables explained only a fraction of global variance in EMF species composition, in contrast with local scale studies of EMF community composition that showed very strong effects of soil environment (Peay *et al.*, 2010b; Taylor *et al.*, 2014; Toljander *et al.*, 2006). Taken together, the preponderance of evidence suggests that the pool of available EMF in a community is set first by the biogeographic history of the region, in which the community is embedded, and that environmental sorting acts as an important filter upon this pool at the local scale.

19.6 Spatial patterns of diversity

Diversity of EMF has been traditionally examined through the lens of local processes – that is, that local conditions at the centimeter or meter scale, such as pH or organic matter concentration, determine the number of EMF in a given sample (Bruns, 1995). However, there are a number of biogeographic hypotheses that predict local richness on the basis of factors that operate and are measured on the scale of kilometers and continents (Ricklefs, 1987). A handful of studies have now evaluated the importance of biogeographic hypotheses explaining diversity patterns in EMF.

The theory of island biogeography (MacArthur and Wilson, 1967) postulates that richness is a function of the effects of island geography on rates of immigration and extinction on that island. The theory is based on population-level processes, where extinction rates are linked to population sizes via island size, and immigration rates are linked to island isolation from potential dispersal sources, such as the mainland. The theory predicts that larger islands should house more species than smaller islands, and that isolated islands should have fewer species than those closer to the mainland. While no studies have examined EMF richness on actual islands in the light of island biogeography theory, Peay and colleagues (Peay *et al*., 2007, 2010a) used a "host island" approach to study island biogeography of EMF (Janzen, 1968). From the perspective of obligate plant symbionts like EMF, non-host plants are inhospitable territory (much like an ocean is to most terrestrial organisms). Host plants can, thus, be thought of as islands in a sea of non-host vegetation.

Using this approach, Peay and colleagues examined patterns of EMF diversity across a landscape in which EMF hosting pines occur patchily in a matrix of AMF shrubs. These patches varied greatly in size (1 to > 10 000 m^2) and in their distance away from a large tract of continuous forest from which spores might disperse (i.e., the "mainland"). They found that EMF diversity patterns corresponded well with patterns expected under island biogeography theory. Species richness of EMF was highest on large host islands and host islands closer to the "mainland".

The increase in species richness with increasing sample area is known as the species area relationship (SAR), and has been described as one of the few laws in ecology. The shape of this relationship is normally modeled as $S = cA^Z$, where S = Species Richness, c is a constant, A is the area sampled, and Z describes the rate at which richness increases with area. There is no doubt that microbial communities are highly diverse, but there has been some debate about whether the species area relationship scales as rapidly as with macrobes. This is important to our view of microbial diversity, as a shallow SAR paints a picture of microbes that are incredibly diverse at small scales (e.g., single soil samples), but with few new species added as new areas are explored.

Some previous work on soil fungi and bacteria found SAR slopes (or z-values) in the range of 0.04–0.07, among the lowest values observed for any taxonomic group (Green *et al*., 2004; Horner-Devine *et al*., 2004). By contrast, Peay *et al*. (2007) estimated a z-value of 0.20 for EMF – more in line with SAR slope values estimated for macrobial organisms such as plants. The nature of this relationship has important consequences for understanding diversity patterns in nature, and in understanding how microbial communities will respond to processes like habitat fragmentation or destruction.

There are still relatively few studies that have estimated SAR for fungi (or EMF). However, our re-analysis of EMF richness from willow host islands on Mount Fuji (Nara *et al.*, 2003) returned a z-value estimate of 0.23. This is probably somewhat of an overestimate, though, as the size of these host islands increased with time, and so larger islands were also older. A very high-intensity sampling and sequencing effort for all soil fungi across grasslands in the Swiss Alps also documented a fairly strong increase in richness with sampling area, and estimated that a minimum area of 16 km^2 would be needed to observe all fungi detected in the study (Pellissier *et al.*, 2014).

As previously mentioned, dispersal is a critical process in most biogeographic models, and yet its role in the ecology of microorganisms has been heavily debated. The dispersal process is not entirely well understood in EMF, in part due to the difficulty of measuring dispersal and in part due to a poor understanding of the behavior of spores in the life cycle of most EMF species. For example, critical details of spore biology, such as germination cues (Nara, 2009), survival ability (Bruns *et al.*, 2009; Peay *et al.*, 2009), and dispersal kernels (Galante *et al.*, 2011), are unknown for most taxa.

There are two parts to the dispersal process – the movement of spores, and their subsequent colonization of host roots. Fungi produce phenomenal numbers of spores, and single fruiting bodies may produce hundreds of millions of spores. However, a number of studies of local-scale dispersal show that spore numbers decrease dramatically with distance away from fruiting bodies, and that the vast majority of spores fall relatively short distances from the fruiting body (Galante *et al.*, 2011; Li, 2005; Peay *et al.*, 2012). Experimental studies indicate that rapid decay in spore quantity can limit the occurrence of EMF on seedlings, beginning from tens (Dickie and Reich, 2005) to hundreds (Peay *et al.*, 2012) of meters. Similar results have been reported as well from saprotrophic fungi (Norros *et al.*, 2012), suggesting that dispersal limitation at the landscape scale is likely a common occurrence in fungi. Read in this context, the prolific spore production by EMF is not an indicator of unlimited dispersal; rather, it is an indication of the difficulty of dispersal.

Large sequence-based datasets also allow for the exploration of major patterns of biogeography to see if they are also consistent in EMF. Perhaps the most well-known spatial diversity pattern is the latitudinal diversity gradient, where most groups of plants and animals peak in diversity in tropical regions. Whether or not such patterns apply to microbial organisms has been unclear. For example, marine microbes tend to peak in diversity at mid-latitudes, as do Bryophytes. Work on EMF has suggested either no gradient (Peay *et al.*, 2010b) or an inverse diversity gradient (Tedersoo and Nara, 2010).

Current results seem to indicate that differences in EMF diversity across latitudes are fairly weak, perhaps with some diversity peaks at mid-latitude northern temperate forests (Tedersoo *et al.*, 2014a). Explaining this result is one of the more interesting challenges in EMF biogeography, and it is possible that deterministic factors, such as climate or soil chemistry, play an important role. However, if EMF diversity is highly dependent on host area, as predicted by island biogeography (Peay *et al.*, 2007), this pattern might result from the low abundance of EMF hosts in many low-latitude forests.

Another possibility comes from the so-called mid-domain effect. The mid-domain effect hypothesis predicts that diversity will be highest in areas where multiple species have overlapping ranges. A recent study from Japan showed that this was true of EMF diversity in mid-elevation montane forests (Miyamoto *et al.*, 2014). While this would not explain the low diversity of EMF in tropical regions, in combination with SAR based-theories it might explain the relatively high diversity in temperate versus boreal forests.

19.7 EMF across time and space

Ectomycorrhizal fungi hail from a diverse evolutionary background, with many independent origins of this lifestyle within the kingdom Fungi (Tedersoo *et al.*, 2010a). While contemporary geographic patterns in community composition and biodiversity are useful, by comparing all lineages at once they ignore the valuable data on the historical processes that structure current distributions, and which can be gained from taking an explicitly evolutionary perspective. These kinds of historical events can be reconstructed using phylogenetic trees based on DNA sequences (Avise *et al.*, 1987; Figure 19.2).

Such analyses require a more specific focus on particular lineages, and are not as yet easily done using bulk environmental sequences, generally requiring significant collections of fungal fruiting bodies. While the results from any particular lineage reflect the chance events that make their evolutionary history unique, evidence from multiple independent lineages provides the basis for strong generalizations. Here, we examine evolutionary evidence at two scales. The first, phylogeography (Avise *et al.*, 1987), uses molecular evidence to reconstruct the historical events that influence modern distributions of a single species or set of closely related sister taxa – generally at the timescale of thousands to millions of years. The second, historical biogeography, attempts to reconstruct the evolutionary events that influence the distribution and diversity of large clades (families, orders) at the scale of tens to hundreds of millions of years, and with respect to key geological events such as the movement of continents and oceans (Lomolino *et al.*, 2006).

Despite the promise of this, field fungi are one of the most poorly studied major taxonomic groups from a phylogeographic perspective (Beheregaray, 2008; Lumbsch *et al.*, 2008). Phylogeoraphic studies of EMF have tended to focus on broadly distributed species or species complexes, primarily in the northern hemisphere. A few key findings appear to be emerging from these studies. The first is that broadly distributed "species" tend, in fact, to be complexes of species, often with non-overlapping geographic ranges. For example, the fly agaric, *Amanita muscaria*, is widely distributed across temperate and boreal forests in the northern hemisphere. Molecular phylogenetics showed that *A. muscaria* is actually a complex of at least three distinct species (Oda *et al.*, 2004) and that, despite the wide variety of *A. muscaria* color morphs, these are not reliable indicators of phylogeny as multiple color morphs occurred in all clades (Geml *et al.*, 2006).

The second finding is that there is generally little geographic overlap in ranges among these species complexes, and little or no evidence for current dispersal between isolated geographic regions (Chapela and Garbelotto, 2004; Nguyen *et al.*, 2013; Oda *et al.*, 2004). Analysis of *Tricholoma matsutake* (Chapela and Garbelotto, 2004) showed that matsutake allies can be clearly differentiated into species groups, and that these groups

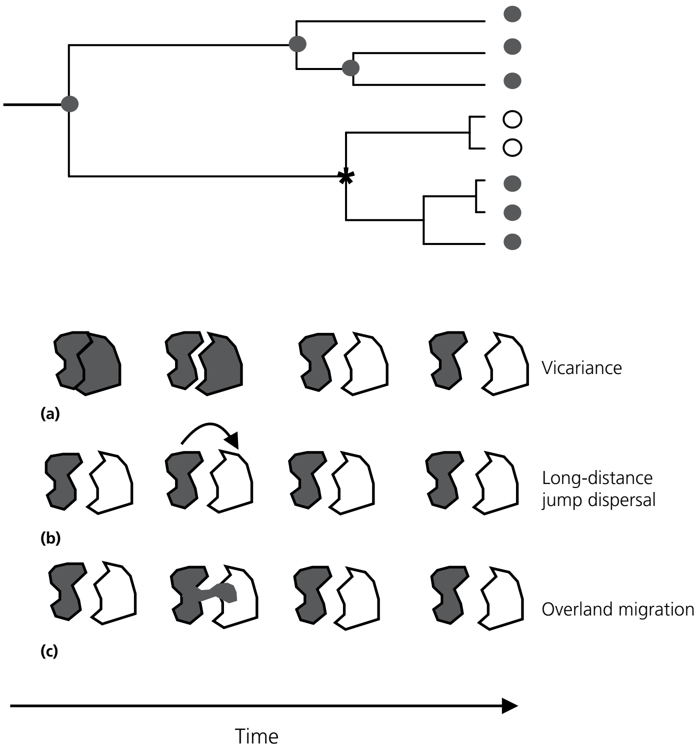

Figure 19.2 The use of molecular phylogenies to infer past events shaping current day distribution patterns in ectomycorrhizal fungi. The phylogeny depicts three different scenarios to explain the modern-day disjunction between species found in the grey and white areas, as indicated by colored symbols at the tips of the phylogeny. Gaps between areas indicate large barriers (oceans, mountains) across which species cannot easily move. Different scenarios depend primarily on the timing of connections between the grey and white areas at the node marked with a*. In scenario (a), the split between grey and white taxa is driven by a vicariant event that breaks up the ancestral range, followed by speciation. In scenario (b), the separation of the two areas predates the origin of the white lineage, and so must result from dispersal (arrow) across the barrier, followed by speciation. In scenario (c), the origin of the white lineages corresponds with the occurrence of a temporary land bridge, suggesting overland migration followed by speciation.

can be clearly differentiated into clades with distinct geographic ranges, including a circumboreal clade, a clade in western North America, eastern North America and then Central America. For *A. muscaria*, the picture is slightly more complicated. All three phylogenetic groups currently coexist in Alaska and are inferred to have a common origin in Beringia. However, different migration histories from Beringia have led to non-overlapping distributions in many parts of the *A. muscaria* range (see Table 19.1).

The third major finding from many of these studies is that current patterns of genetic diversity and distribution appear linked to the recent history of glaciation and recolonization. The few EMF lineages that have been examined appear to have northern origins during the Neogene. Both *T. matsutake* and *A. muscaria* originated in humid

Table 19.1 A summary of recent ectomycorrhizal biogeography studies based on molecular data. Mean or median age (million years) of crown groups are reported for each clade, with 95% highest posterior density (HPD) in parentheses. Where multiple estimates are available only the most recent is given.

Taxon	**Ancestral range**	**Clade age MYA (HPD)**	**Geographic structure**	**Primary dispersal modes**	**Sources**
Tuber	Eurasia	142 (122–162)	Yes – many endemic clades in Europe. Distinct sister lineage present in Southern hemisphere.	Primarily intra-continental migration (Asia, Europe) and via landbridge migration to N. America	Bonito *et al*. (2013) Jeandroz *et al*. (2008)
Inocybaceae	Paleotropics	60 (40–80)	Yes – Some likely vicariance events (Africa-India), limited clade diversity in S. America.	Some boreotropical migration, possible jump dispersal for Australian and temperate S. American lineages.	Ryberg and Matheny (2011) Matheny *et al*. (2009)
Amanita sect. *Caesareae*	Paleotropics	56 (39–73)	Yes – most species occur in clearly differentiated regional groups.	Primarily overland consistent with boreotropical migration.	Sánchez-Ramírez *et al*. (2015)
Sclerodermatineae	Asia/North America	82 (60–115)	Yes – at the individual species level but most clades old enough for broad distribution.	Very broad ancestral range, with some pantropical lineages consistent with boreotropical migration. Frequent long-distance dispersal.	Wilson *et al*. (2012)
Hysterangiales	Gondwana	Not dated	Yes – endemism at species level but geographic split only evident at deep nodes between northern and southern hemisphere.	Initially broad ancestral range, frequent long-distance dispersal.	Hosaka *et al*. (2008)
Austropaxillus-*Gymnopaxillus* (Serpulaceae)	Western N.A. (Serpulaceae)	22 (32–12)	Yes – Australasian clade nested within north temperate clade	Long-distance dispersal; *in situ* diversification in Australasia	Skrede *et al*. (2011)
Porcini clade	Palaeotropical	42 (23–62)*	Yes – lineages rare in southern hemisphere	Episodic long-distance dispersal	Dentinger *et al*. (2010)
Cortinarius violaceus group	Australasia	14 (18–10)	Yes – north and south American lineages nested within an Australasian clade	Long-distance dispersal and founder-event speciation	Harrower *et al*. (2015)
Clavulina	Tropical	Not estimated (relative rates used)	Yes – temperate clades derived from tropical groups	Not addressed	Kennedy *et al*. (2012)
/Sebacina (Sebacinales)	North America	57–45 MYA	Yes – four major biogeographic groups detected	Strong impact of dispersal limitation on large scale; recent dispersal in northern Holarctic and to Mediterranean and southern hemisphere	Tedersoo *et al*. (2014b)

* Slightly older dates are also reported, based on a different calibration point.

temperate forests that occurred in the north, and then migrated southward as the climate cooled. Some of the current genetic differentiation is interpreted as being the result of persistence of species in glacial refugia and their separation by non-host vegetation. Murat *et al.* (2004) also showed that, for European *Tuber melanosporum*, genetic diversity closely correlated with location of suspected glacial refugia, and that migration of current genotypes can be tracked along suspected host migration routes. The effects of glaciation are also evidenced by low allelic diversity resulting from bottlenecks. The fact that gene flow seems to follow host migration routes is also good evidence for the effectiveness of mountains or oceans as dispersal barriers (Amend *et al.*, 2010).

One interesting exception may be the arctic fungi (both EMF and non-EM), which appear to show relatively frequent transcontinental dispersal, perhaps due to the extreme effects of climate change at high latitudes and the need for very large dispersal events to track them (Geml, 2011). Consistent with this, EMF communities on the arctic island of Svalbard show evidence for frequent long-distance, transoceanic colonization events (Geml *et al.*, 2011).

In general, the use of phylogeography to identify current hotspots of genetic diversity appears to match well with what is known about locations of glacial refugia from plant studies. While it does seem as if these studies all show a concordance between host migrations and EMF migrations, it is not clear if the fungi are limited by or tracking the host plants, or if both plant and fungal populations are equally limited by the same dispersal barriers.

As for phylogeography, there are still few studies that have attempted to reconstruct the evolutionary history of fungi over geological time scales. The field has developed slowly, in part because the fossils that play an important role in documenting the presence or absence of particular forms as continents joined and split are not suitably abundant for fungi to reliably document their distributions. However, the few fossilized fungi that are available (e.g., Boyce *et al.*, 2007; Hibbett *et al.*, 1995) can be incredibly useful as anchor points to calibrate the time scale in molecular phylogenies, and help provide more accurate dates for key events.

With historical biogeography, the timing of splits between lineages (e.g., the origin of a new node in the tree) with respect to the position of the continents is critical in understanding the manner in which current distributions (and, in particular, disjunct distributions) arose. If the nodes originated prior to the breakup of a landmass or the origin of a dispersal barrier (e.g., orogeny), the disjunction most likely represents allopatric speciation; however, if the node arises after the breakup, the disjunction must result from long-distance dispersal (de Queiroz, 2005). The timing of these events can provide insight into the biology and selection processes that are unique to EMF. For example, some key questions are how common is long-distance dispersal in EMF, is the distribution of EMF determined primarily by the distribution of particular hosts, and where and when did most EMF lineages originate?

Broadly speaking, it appears that most major fungal lineages (e.g., at the family or order level) are old enough to have global distributions. For example, the same EMF genera (*Russula*, *Tomentella*, *Lactarius*, *Inocybe*) are dominant players in neotropical rainforests and paleotropical rainforests, as well as in temperate and boreal forests, despite the fact that few of these systems appear to share any biological species. While AMF have been around since plants first colonized the land, ectomycorrhizal symbiosis likely did not originate until ≈ 270–130 MYA, based on molecular dating of fungal and plant phylogenies (Hibbett and Matheny, 2009).

The EMF habit has originated numerous times (Tedersoo *et al.*, 2010a) independently from saprotrophic ancestors (Wolfe *et al.*, 2012). The transition from saprotrophy to ectomycorrhizal symbiosis involves profound genomic changes, including the loss of genes coding for plant cell wall degrading-enzymes and an increase in genes for secreted effector-like proteins that mediate host interactions (Kohler *et al.*, 2015). Once evolved, though, the EMF habit generally appears to be stable, and reversion to saprotrophy is uncommon (Bruns and Shefferson, 2004).

Given the unique nutritional aspects of the symbiosis, understanding when and where the ectomycorrhizal habit evolved will give fundamental insight into the selective pressures that lead to this lifestyle transition. This is an important question in Earth's history, as the presence of ectomycorrhizal symbiosis has strong impacts on geochemical cycles (Averill *et al.*, 2014; Clemmensen *et al.*, 2013). While it is easy to think of EMF as primarily a north temperate association, based on phylogeographic studies a number of EMF groups, including the Inocybaceae (Matheny *et al.*, 2009), *Amanita* sect *Caesareae* (Sánchez-Ramírez *et al.*, 2015) and Sclerodermatineae (Wilson *et al.*, 2012), show evidence for paleotropical origins. The diversity of lineages with paleotropical origins may provide important clues to the conditions under which EMF symbiosis can arise as a successful ecological strategy for both plants and fungi.

Historical biogeography studies also show that, for most large lineages of EMF, there are strong patterns of regional endemism, with most species and many clades restricted to single continents (Bonito *et al.*, 2013; Hosaka *et al.*, 2008; Matheny *et al.*, 2009). The geographic range of individual clades within EMF groups can also vary significantly. Within the Tuberaceae, the majority of clades are restricted to single continents, but a few, such as the black truffle\melanosporum clade, are widely distributed across Europe, Asia and North America (Bonito *et al.*, 2013). The degree of endemism also varies, depending on taxonomic scale. The Hysterangiales show clear evidence of separate Holarctic and Gondwanan lineages, but groups within the Holarctic appear to be broadly distributed across Europe, North and Central America.

As suspected by early fungal biogeographers (Pirozynski, 1983), there does appear to be a unique set of southern hemisphere fungi. For example, within the Tuberaceae, the genus *Tuber* is found primarily in the Northern Hemisphere, while a distinct set of sister taxa are found in Australia, New Zealand and southern South America. In this case, the estimated divergence date between northern and southern lineages, around 156–160 MYA corresponds with the breakup of Pangaea into the Gondwanan and Laurasian landmasses (Bonito *et al.*, 2013).

Disjunct distributions are present in nearly every phylogenetic reconstruction used in EMF historical biogeography. While there are some splits (e.g., *Tuber*) that match the timing of known vicariance events, such as the breakup of Pangaea, there are many others that do not. These non-vicariant disjunctions provide evidence that, over geological time frames, EMF are quite capable of long-distance dispersal. For example, the timing of origin of some nodes associated with *Inocybe* species in Australia and New Zealand is incompatible with vicariance and, therefore, must have arisen from transoceanic dispersal (Matheny *et al.*, 2009). Neotropical species of the *Cortinarius violaceous* group appear to have arisen from a long-distance dispersal event from Australia within the last 13–7 million years (Harrower *et al.*, 2015). Molecular genetic evidence for saprotrophic fungi is also consistent with episodic transoceanic dispersal events throughout the southern hemisphere (Moncalvo and Buchanan, 2008).

Along with the evidence for transoceanic spore movement, many of the current disjunctions in EMF appear to have arisen from overland migration and subsequent speciation. One scenario, the boreotropical hypothesis, suggests that many groups reached their current distributions during the late Miocene, when tropical forests extended north into areas that are currently temperate. At higher latitudes, dispersal between Europe, Asia and North America was then possible through land bridges in places such as Beringia. A very nice example of the boreotropical hypothesis comes from divergence dating of EMF lineages within *Amanita* sect. Caesarea (Sánchez-Ramírez *et al.*, 2015). Based on the timing and geographic location of divergences, Sánchez-Ramírez *et al.* were able to reconstruct an overland migration route out of tropical Africa ≈ 20–16 MYA, migration through southeast Asia to east Asia 8–4 MYA, and then migration across Beringia into the pacific northwest of N. America around 3 MYA.

19.8 Conclusions

The field of EMF biogeography is still young, as it requires molecular tools that have only recently been developed. However, in the last decade, we have already learned a great deal. The pre-molecular view of unlimited dispersal has been rejected and replaced by a much more nuanced view of ectomycorrhizal ecology and evolution. Current patterns of EMF distribution reflect the importance of dispersal barriers and the unique timing and geological context in which individual lineages arose, migrated and evolved. The presence of northern migration routes between Asia and North America, and the migration of host trees with climate and ice ages, are evident in EMF phylogenies.

While long-distance dispersal events have occurred, and are certainly important in EMF, it is not clear that they are disproportionately important, compared with the role of long-distance dispersal in plant (Higgins *et al.*, 2003) or animal (Springer *et al.*, 2011) biogeography. In fact, it has been recently argued that long-distance dispersal events have been more common and important in the shaping the biogeography of plants and animals than previously suspected (de Queiroz, 2005, 2014). Similarly, the richness of EMF communities does not seem to follow those of plants or animals at the global or continental scale (i.e., latitudinal diversity gradient), but these exceptions appear to be driven by similar underlying principles. For example, low diversity of EMF in some tropical forests may be caused, in part, by low host abundance and species area effects. Identifying these exceptions may help elucidate the unique ways in which EMF physiology responds to climate or environment, and shed light into the fundamental nature of this symbiosis.

While much has been learned up to this point, this is still an exciting time for studying EMF biogeography. We are in the lucky position of having to cope with a flood of incoming molecular data from all parts of the globe, and a variety of data streams (environmental samples, mushroom collections, genomes). There are a number of emerging challenges that could be addressed with these data.

First, while biogeographic regions have been primarily delimited using macroorganisms, there is no comparable picture for soil fungi. The abundance of environmental sequence data could quite feasibly be used to delineate major biogeographic regions for EMF (Kreft and Jetz, 2010).

Second, despite the early interest in Gondwanan fungi expressed in the pre-molecular era, there still have been only a handful of molecular EMF biogeography studies, and there is a paucity of data examining fungi with purported Gondwanan origins. In addition, perhaps an inordinate amount of research has been focused on lineages of EMF that are edible or have human cultural significance (e.g., *Tuber*, *Boletus edulis*, *Tricholoma matsutake*, *Amanita caesarea* and *Amanita muscaria*). Biogeography of putatively old, dominant EMF lineages, such as the Thelephoraceae or Russulaceae, would shed a great deal of light into the origins and evolutionary history of the symbiosis.

As data from new lineages accumulate, it will be possible to search more rigorously for general patterns. How does the symbiotic lifestyle shape the biogeography of EMF? How do these patterns differ from saprotrophic fungal lineages that may be older or less constrained by host associations? What ecological features predispose particular EMF to long-range spore dispersal or long-distance migration? In addition, many classic biogeographic patterns have yet to be examined through the lens of EMF. For example, to what degree do EMF respect traditional biogeographic barriers, such as Wallace's line, the deep channel between continental shelves that sharply demarcates the fauna of southeast Asian origin from those of Australian origin?

Finally, biogeography has an important role to play in the current era. In particular, our understanding of the biogeographic history of EMF will help to identify invasive species more quickly, and also to understand the importance of EMF in mediating the invasion of exotic tree species. While "microbes" are not generally at the top of conservation concerns, the understanding that most EMF have spatially restricted ranges, and that loss of host area could reduce their diversity, suggest that native EMF diversity may require conservation action to protect. These fungi have much to teach us about the history of our planet and, with the new eyes provided by modern molecular tools, all we need to do is look.

19.9 References

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