MICROBIOME

Dimensions of biodiversity in the Earth mycobiome

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Abstract | Fungi represent a large proportion of the genetic diversity on Earth and fungal activity influences the structure of plant and animal communities, as well as rates of ecosystem processes. Large-scale DNA-sequencing datasets are beginning to reveal the dimensions of fungal biodiversity, which seem to be fundamentally different to bacteria, plants and animals. In this Review, we describe the patterns of fungal biodiversity that have been revealed by molecular-based studies. Furthermore, we consider the evidence that supports the roles of different candidate drivers of fungal diversity at a range of spatial scales, as well as the role of dispersal limitation in maintaining regional endemism and influencing local community assembly. Finally, we discuss the ecological mechanisms that are likely to be responsible for the high heterogeneity that is observed in fungal communities at local scales.

Next-generation sequencing
(NGS). A set of DNA-sequencing platforms (including those produced by 454 and Illumina) that have increased sequencing output and decreased cost by orders of magnitude compared with Sanger sequencing.

Monophyletic
A group of organisms that consists of an ancestor and all of its descendants. Monophyly is the basis for modern taxonomy.

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If you look closely at any terrestrial scene, you will see fungal hyphae twisting around plants[1], animals[2], soil[3,4] and even bacteria[5] (FIG. 1). Although not often obvious to the naked eye, fungi are as deeply enmeshed in the evolutionary history and ecology of life as any other organism on Earth. The evolution of arbuscular mycorrhizal root mutualisms facilitated the colonization of land by plants approximately 500 million years ago[6], and the evolution of fungal peroxidases that are capable of degrading lignin (the most recalcitrant plant cell wall polymer) approximately 300 million years ago fundamentally altered carbon cycling in soils[7]. Furthermore, the influence of fungi can be seen in the genomes of all plants[8], in the function of human immune systems[9] and in the chemistry of the soils beneath our feet[10]. For example, the long-running evolutionary 'arms race' with fungal pathogens has been instrumental in maintaining the high taxonomic diversity of plant species that are found in tropical forests[11]. Despite the pervasive influence of fungi on Earth processes, we have only recently begun to appreciate the true magnitude of fungal diversity. However, following the development of next-generation sequencing (NGS), large-scale DNA-sequence datasets have recently become available that have revised estimates of fungal diversity (BOX 1) and provided a new understanding of how fungal diversity shapes, and is shaped by, other ecosystem components.

True fungi belong to a monophyletic kingdom that diverged from animals approximately 1 billion years ago[12]. Collectively, organisms in the fungal kingdom and the habitats that they occupy make up the 'mycobiome' (FIG. 1). The hallmark of fungi is the presence of hyphal growth: the ability to form a network of interconnected filaments (known as a mycelium) as primary somatic tissue. Single-celled fungi[2] can predominate in some liquid or stressful environments[13], such as anaerobic gut rumen[14], floral nectar[15] or deep marine sediments[16], in which filamentous growth may be disadvantageous. However, hyphal fungi represent the greatest diversity and highest abundance of fungi in natural systems[3,4,17]. The hyphal lifestyle means that fungi can perceive and respond to the environment at the micrometre scale and, at the same time, share resources and coordinate activity across the heterogeneous environments that are spanned by each mycelium[18]. Owing to the size of these mycelia, the mycobiome may include some of the largest (and oldest) individual organisms in nature[19], with reports of clones that extend over an area >1,000 ha in size and that are more than 1,000 years in age. As osmotrophs, fungi are efficient decomposers of organic matter and they produce a potent and diverse array of organic acids and enzymes that can dissolve and recycle some of the most recalcitrant natural[7] and man-made[20] materials.

Thus, the evolutionary and ecological success of fungi is driven by a unique combination of morphological and biochemical features that sets them apart from other organisms. Considering fungal ecology in the light of fungal biology is therefore a crucial step in understanding the emerging patterns of fungal biodiversity that are generated from DNA sequencing of the mycobiome[21,22]. In this Review, we describe these patterns of fungal biodiversity, including variations in the species richness, composition and function of different fungal communities, and we discuss how this biodiversity might be

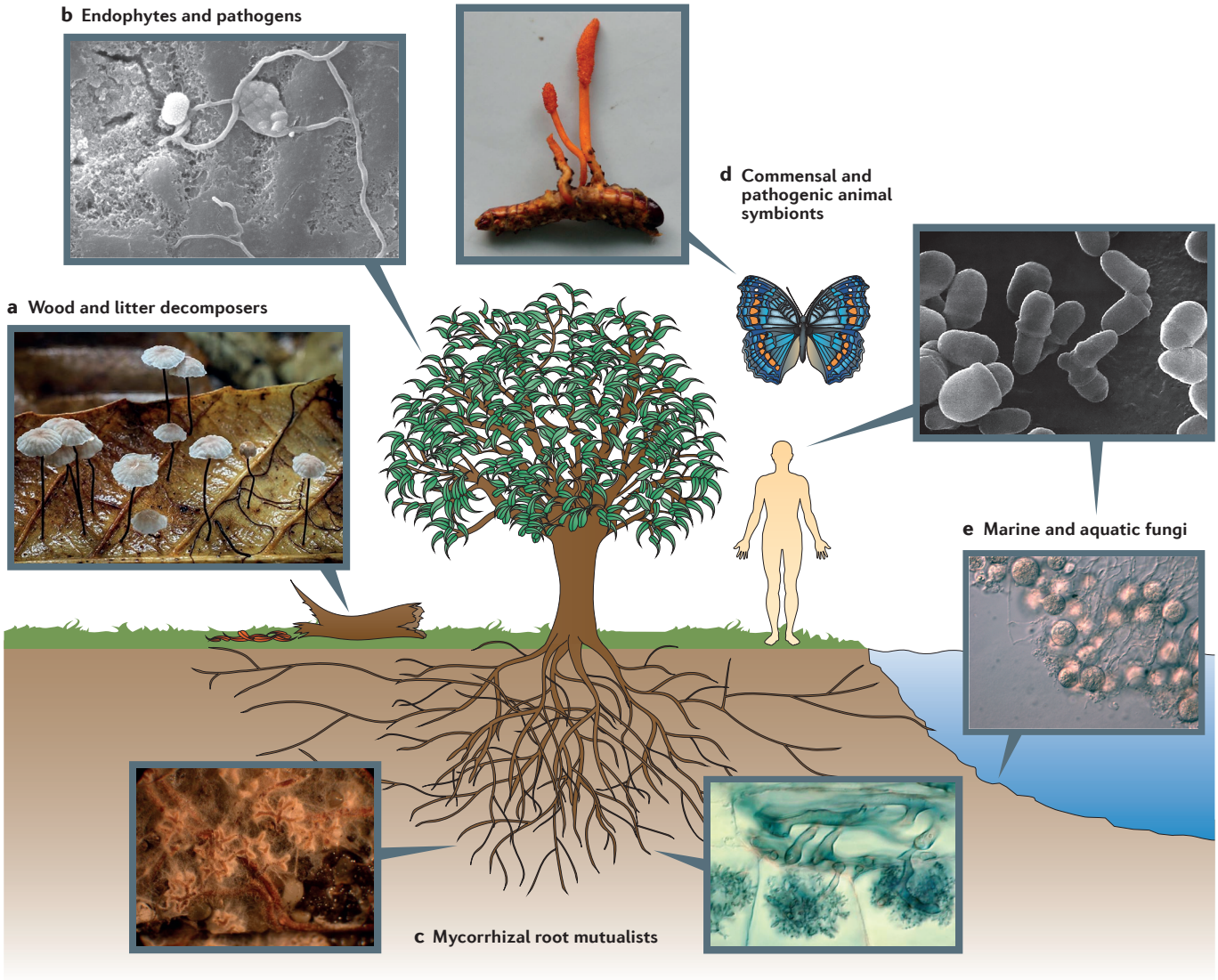


Figure 1 | **Functional diversity of the mycobiome.** Fungi are most commonly associated with terrestrial ecosystems, but can also be found growing on nearly any substrate on Earth, from deep ocean sediments to the human scalp. **a** | The majority of fungal species are saprotrophs that are capable of decomposing complex polymers, such as cellulose and chitin, although individual species can vary considerably in both the substrates that they decompose and the enzymatic pathways that they use. In both terrestrial and freshwater systems, fungi can dominate the decomposition of plant necromass. **b** | Fungi are commonly found inside living plant cells, either as endophytes or pathogens. Although fungal pathogens have long been known and feared, molecular tools are only now revealing a hitherto unknown diversity of endophytic fungi, which grow asymptomatically inside the cells of plant roots, stems and leaves. **c** | Fungi are prominent plant mutualists, with the majority of land plants forming symbioses known as mycorrhizae ('fungus roots') with fungi to increase nutrient uptake through physical and chemical means. Similarly to most other fungal functional guilds, mycorrhizal fungi are highly polyphyletic. Mycorrhizal fungi can be further divided into ectomycorrhizal fungi (shown on the left), arbuscular mycorrhizal fungi (shown on the right), ericoid mycorrhizal fungi and orchid mycorrhizal fungi, each of which is associated with distinct physiological capabilities. **d**,**e** | The diversity of fungi that live in association with animals and in aquatic environments is less well explored, in part because fungi are far less abundant than bacteria in these systems. These fungal communities are often dominated by single-celled members of the Ascomycota and Basidiomycota phyla. Some fungal genera are found in both animal and marine mycobiomes, such as *Malassezia* spp. (shown here is a scanning electron micrograph of *Malassezia lipophilis*). Although fungi are primarily commensal in animals, notable exceptions include the insect pathogen *Cordyceps formosana*, the fruiting bodies of which are shown emerging from the host insect (part **d**). Aquatic environments contain novel fungal lineages, illustrated in the figure by a chytrid fungus, that may contain clues to the evolutionary origins of fungi (part **e**). Endophyte scanning electron microscope image in part **a** courtesy of E. Burns, Save the Redwoods League, California, USA. *Gymnopus quercophilus* image in part **b** courtesy of F. Stevens, Mykoweb.com, California, USA. Ectomycorrhizal root image in part **c** courtesy of K.G.P. Arbuscule image in part **c** courtesy of M. Brundrett, Department of Parks and Wildlife, Swan Region, Australia. *Cordyceps formosana* image in part **d** courtesy of C. Alisha Quandt, University of Michigan, USA. Chytrid image in part **e** courtesy of T. James, University of Michigan, USA.

Osmotrophs
Organisms that rely on the uptake of dissolved organic compounds for their primary nutrition.

Chitin
A polymer of *N*-acetylglucosamine that is an important component of fungal cell walls.

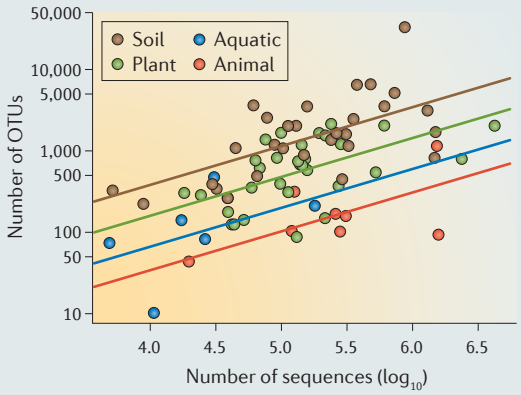
influenced by the unique biology of the mycobiome. Importantly, we consider how fungal biodiversity is partitioned across different habitats and temporal and spatial scales. Finally, we compare the patterns of biodiversity of the mycobiome with those of the bacterial component of the microbiome, which differ in several fundamental respects.

Diversity of mycobiomes

The diversity and composition of the mycobiome change profoundly across environments. Exploration of fungal diversity has been greatly facilitated by the development of NGS (BOX 1), which has enabled the identification of fungi from thousands of DNA samples taken from all regions of the world. The majority of published NGS datasets that provide insights into total fungal richness are from studies that examine fungi in soil or plants, with few high-quality NGS datasets available for examining fungal diversity in animals or aquatic ecosystems (Supplementary information S1 (table)) — environments that have largely been ignored by fungal ecologists. This research bias generally fits in with the existing perception that both fungal biomass and diversity are greatest in soils and plants, and that the greatest contribution of fungi to the function of ecosystems is therefore to be found in these environments[23,24]. Indeed, based on current data, fungal diversity seems to be highest in soils (BOX 1). The most comprehensive survey of global fungal diversity to date identified >80,000 species of soil fungi[4], and surveys of just a few grams of soil frequently detect

Box 1 | **Molecular approaches to describing and quantifying fungal diversity**

Morphology-based approaches to understanding fungal diversity are greatly hampered by our inability to culture most fungi isolated from natural environments, the lack of taxonomically informative morphological features on hyphae and the infrequent production of diagnostic sexual structures either in culture or the environment. However, the study of fungal diversity has advanced substantially with the use of molecular-based approaches, specifically culture-independent methods that rely on the amplification of taxonomic marker sequences by PCR. The internal transcribed spacer (ITS) region of the nuclear rRNA operon has been designated the official taxonomic barcode for Fungi[113] and provides species-level taxonomic delineation. Although the most commonly used ITS primers provide broad coverage of the fungal kingdom, biases inherent to the amplification of ITS, as with any taxonomic marker sequence, result in the under-representation of particular taxonomic groups. For this reason, detailed ecological studies of some basal fungal lineages or arbuscular mycorrhizal fungi are often carried out using additional primers or gene regions, such as from the genes that encode the large or small ribosomal subunits.



As taxonomic marker sequences do not correspond directly with the biological species concept in fungi, a sequence similarity threshold is used to define operational taxonomic units (OTUs) that can be used as the basis for ecological studies. The threshold used may vary between studies, genes or taxa, but is often 96–99% for ITS (and for other marker sequences from rRNA operons). However, although the use of ITS as a marker enables the accurate classification of fungi to a near species level (as opposed to the 16S rRNA marker gene that is used to classify bacteria, which is more analogous to a genus-level or family-level marker), in some cases a standard similarity threshold may still group ITS sequences from ecologically distinct species into a single OTU[42]. A second limitation is that common bioinformatics pipelines are, for the most part, not optimized for dealing with some of the unique features of ITS, such as sequence length heterogeneity.

Despite limitations, the use of molecular approaches has revealed a great deal about the diversity of the mycobiome and has corrected three fundamental misconceptions that arose from the inability to accurately distinguish species based on morphological features: underestimation of the magnitude of fungal diversity, mistaken inference of cosmopolitan species distributions and skewed estimation of species abundances in communities. In addition to the more accurate estimation of fungal diversity that is provided by molecular approaches, our view of fungal communities has been further transformed by progressive increases in sequencing power that have enabled an increasing number of samples and habitats to be characterized, and at greater sequencing depth.

To illustrate how molecular approaches and improved sequencing power have transformed our view of fungal biodiversity, consider the question 'what is the true magnitude of global diversity of the mycobiome?' DNA sequencing has shown that a previous estimate of 1.5 million species, which was extrapolated from a 6/1 ratio of known fungal and plant species in the United Kingdom[114], was undoubtedly an underestimate. As a general rule, estimates of fungal diversity increase with sequencing and sampling depth (see the figure), with perhaps the most comprehensive census of soil fungi and plants to date finding a fungal/plant species ratio of 17/1, which extrapolates to 6 million species[115]. However, fungal/plant species richness ratios seem to decrease with latitude[4,116] and may not always be correlated[117], which complicates global extrapolations. In addition, global estimates largely ignore animal and marine environments, which have a greater diversity of fungal species than previously suspected[23,31]. However, a study that used ITS sequencing to quantify fungal communities from the same habitat (alder forests), but located across a range of latitudes, was able to assess fungal diversity at large spatial scales without habitat specificity as a confounding factor[111]. In this study, ectomycorrhizal fungal richness patterns were largely consistent across nearly 100 sites, which suggests that scaling regional estimates of β-diversity in different habitats to a global scale may be feasible.

Box 2 | **Diversity in the human mycobiome**

Despite the importance of fungi as agents of disease[118], knowledge about the richness, composition and biogeography of the human mycobiome has lagged behind that of the bacterial component of the human microbiome. This is largely a result of the relatively low abundance of fungal DNA on most bodily surfaces[24], which has made culture-independent analyses more challenging. However, as DNA extraction procedures and sequencing technologies have improved, the human mycobiome has been better characterized and several patterns have begun to emerge[119]. Similarly to the bacterial component of the human microbiome, the mycobiome shows clear variation between internal and external body sites: yeasts such as *Candida* spp. are relatively common in the gut, lung and oral cavity, whereas skin surfaces are often dominated by species from the *Malassezia* genus[2,119]. Unlike the bacterial component of the skin microbiome, the composition of the skin mycobiome was substantially better explained by body site location than by site physiology[2]. Variation in fungal community composition and diversity has also been observed between individuals[33] and according to health state[120]. Although the overall abundance and species richness of fungal communities does generally seem to be much lower than that of bacterial communities in healthy individuals, fungi can represent a dominant proportion of the total microbiota in infected wounds or in immunocompromised patients[121]. Ecological interactions with commensal bacteria can also influence the human mycobiome. Increases in infections caused by *Candida* spp. following the use of antibiotics have long been known[120] and, more recently, dysbiosis of the gut microbiota has been associated with changes to the mycobiome in mice[122]. Looking forward, community transplant experiments[108] will be a key next step if we are to assess how different resources and conditions influence the assembly, richness and composition of the human mycobiome.

hundreds of fungal species[4,25,26]. The high fungal diversity in soil is probably due to the radiation of fungal taxa into an open ecological niche when terrestrial ecosystems first developed[27]. Although all of the major branches of the fungal kingdom are frequently recovered from soil, this habitat is notable for a relatively high abundance of Basidiomycota and mycorrhizal fungi compared with other fungal habitats.

Living plant tissues are also exceptionally rich in fungal species, with leaves, stems and roots of plants being heavily colonized by various endophytic fungi, mycorrhizal fungi and fungal pathogens. For example, >2,500 taxa of endophytic fungi were recovered from the leaves of a single native tree species in Hawaii[17], the Ohia lehua (*Metrosideros polymorpha*). The root systems of a single tree can harbour >100 species of ectomycorrhizal fungi[28] and dozens of endophytic fungal species have been detected from single leaves[1]. The dominant taxa of endophytic fungi do not substantially overlap between leaf-associated and root-associated communities. Leaf-associated fungal communities seem to be dominated by members of the phylum Ascomycota (although basidiomycete yeasts and rusts can also be very common), whereas the composition of root-associated fungal communities varies greatly depending on the type of association: Glomeromycota dominate arbuscular mycorrhizal communities, Basidiomycota dominate ectomycorrhizal communities and Ascomycota dominate communities of ericoid mycorrhizal fungi or root-associated endophytic fungi[29]. Interestingly, both root-associated and leaf-associated endophytic fungi are frequently detected in soils and many endophytic fungi are successful opportunistic decomposers soon after litterfall; however, these endophytic fungi are probably outcompeted rapidly by endogenous soil fungi, which have a greater ability to decompose the recalcitrant organic matter that is found in leaves.

Basidiomycota
One of the major phyla of the fungal kingdom, which includes some of the most dominant fungal species in natural systems and many key ectomycorrhizal and wood-decomposing taxa. Most fungal species that produce prominent mushrooms are from the Basidiomycota.

Mycorrhizal fungi
Fungi that are in symbiotic associations with plant roots, based on the exchange of photosynthates for soil nutrients, such as nitrogen and phosphorous.

Endophytic fungi
Fungi that live asymptomatically inside plant tissue.

Ectomycorrhizal fungi
Fungi engaged in a common form of mycorrhizal symbiosis that is characterized anatomically by fungal hyphae that wholly enclose the fine roots of the host. Ectomycorrhizal fungi evolved from several different lineages and many retain the decomposing abilities of their saprotrophic ancestors.

Current data from fungal NGS studies are consistent with a generally lower level of fungal diversity in animal and marine environments than in soil and plants (BOX 1; Supplementary information S2 (box)). However, the total fungal diversity of animal and marine habitats may be underestimated, owing to a combination of a lack of large-scale sequencing studies from these environments and the tendency for a lower species richness to be reported for habitats for which the sequencing depth is low. Furthermore, animal and marine habitats contain many novel lineages[23,30], which indicates that fungal phylogenetic diversity and function in these environments may be greater than previously suspected[31]. For example, recent investigation of freshwater ecosystems helped to reveal the existence of the Cryptomycota, which is a newly proposed phylum that may represent the earliest diverging clade of true Fungi[30]. These single-celled fungi are capable of forming flagella and are parasites of other fungi and algae[30]. Interestingly, the disparate habitats of marine sediments and human skin tend to be dominated by just a few genera of yeasts in the Ascomycota and Basidiomycota[16]. For example, some species of *Candida*, in the Ascomycota, cause thrush and vaginitis and some species of *Malassezia,* in the Basidiomycota, cause dandruff, whereas other species from these two genera seem to dominate fungal communities that are associated with corals and marine sediments[23,32]. Despite these interesting findings, caution should be exercised when interpreting NGS data from low-biomass systems, such as marine and animal mycobiomes, as sequencing artefacts and DNA from spores or contaminants can have marked effects on the results. For example, sequences that correspond to mycorrhizal fungi have been reported in an NGS study of samples from the human mouth[33], even though mycorrhizal fungi do not actively grow in this environment, as noted by the authors of the study. Furthermore, although interest in the human mycobiome has increased (BOX 2), many sequencing studies use taxonomic markers that are too coarse to be useful for the analysis of species biodiversity.

The notable differences that are observed in the compositions of fungal communities across environments seem to be linked to the advantage that is provided by hyphal growth for osmotrophy in solid substrates, such as soil or woody plant tissue. This morphological innovation and the ability to form symbioses with living plants has led to the ecological success of hyphal fungi in many of the new niches that were created during the formation of terrestrial ecosystems.

Drivers of global biodiversity

Increasing evidence from NGS studies suggests that the composition of the mycobiome is markedly affected by ecological and evolutionary factors that operate at the scale of hundreds to thousands of kilometres. In addition to the high local diversity of fungi in a given sample (see above), these spatial changes in fungal composition are now recognized as a large contributor to the total diversity of the global mycobiome (FIG. 2).

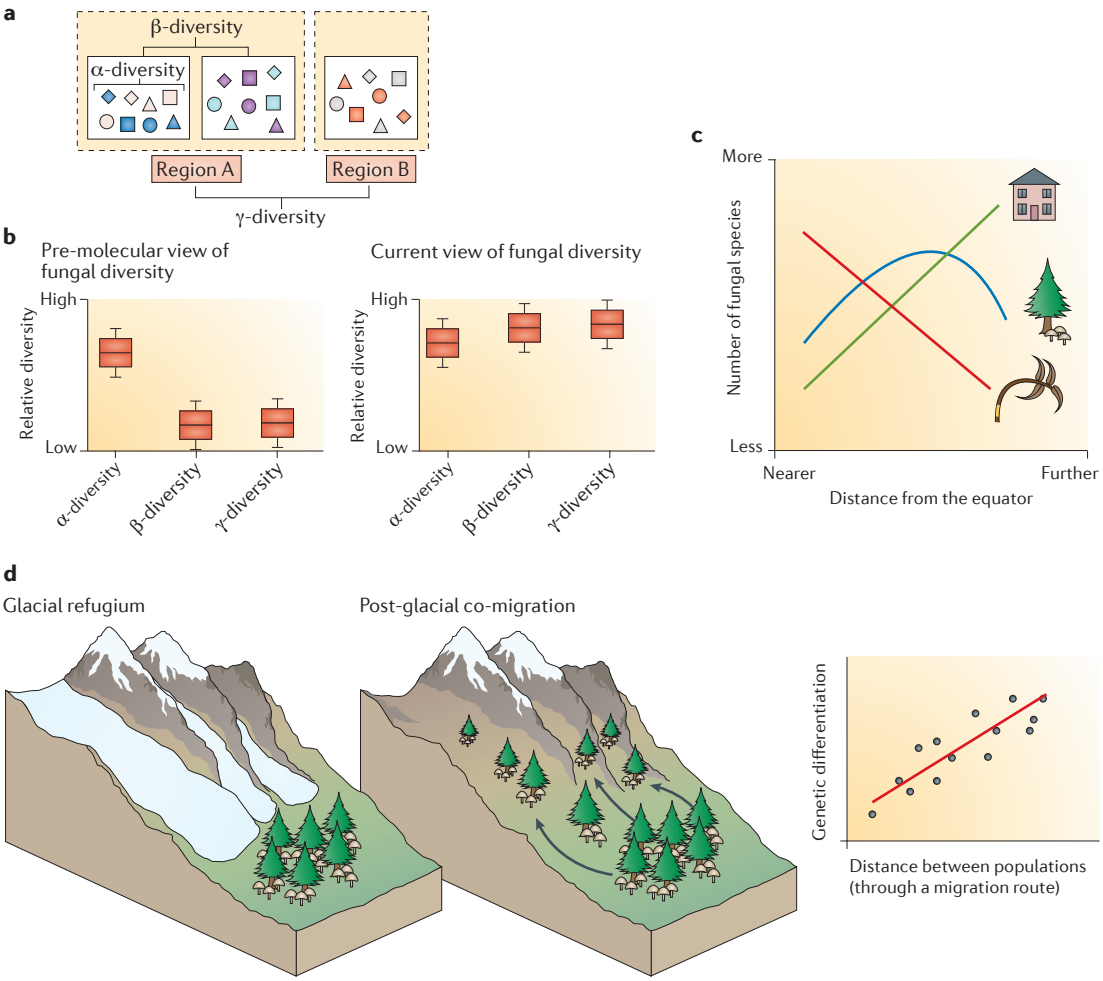


Figure 2 | **Biogeography and emerging views of fungal diversity. a** | Diversity can be measured as the number of species in a single sample (α-diversity), the difference in species between individual samples (β-diversity) or total, or regional, diversity (γ-diversity). **b** | Views of fungal diversity in the literature have changed with the use of molecular approaches to study the mycobiome. Pre-molecular studies tended to emphasize α-diversity as the most important component of fungal diversity, whereas molecular studies have shown that high β-diversity contributes to various macroecological patterns, such as strongly positive species–area relationships and the geographical differentiation of fungal communities. As a result, these molecular approaches have led to increased estimates of the level of γ-diversity in the mycobiome. **c** | The latitudinal gradient in species diversity is one of the most studied macroecological patterns. In contrast to the decreasing diversity with latitude that is seen for most macroorganisms, for which species richness is highest in the tropics, the latitudinal gradient of species diversity for fungi varies according to the taxon and functional guild that are investigated. For example, fungal pathogens have been shown to decrease in diversity with latitude (red line), whereas fungi in the built environment have been shown to increase in diversity with latitude (green line). Furthermore, the latitudinal gradient of species diversity for fungi is not always linear, as shown here for ectomycorrhizal fungi, which have been shown to have a unimodal diversity gradient (blue line). **d** | The evolution of new species or genetic diversity in fungi is often associated with dispersal or migration into new habitats. A hypothetical example of a migration into a new habitat is shown, in which post-glacial co-migration occurs of an ectomycorrhizal fungal species and a host tree species into two valleys that are separated by a mountain range. Over time, the geographical separation of the two populations leads to an increase in genetic differentiation along the migration route. Similar patterns of migration, genetic differentiation and, eventually, speciation have been observed for the co-migration of fungi and host trees across the Bering land bridge into North America.

Ascomycota
One of the major phyla of the fungal kingdom. Some of the most dominant fungi in natural systems are found in this phylum, including many agriculturally important pathogens and most fungi that form lichen.

Rusts
A group of plant pathogens that are obligate biotrophs characterized by complex life cycles that involve several plant hosts. Rusts infect many agriculturally important crops, such as coffee, soybean and wheat, producing reddish-brown spores that give infected hosts the appearance of being rusty.

Glomeromycota
The phylum to which all arbuscular mycorrhizal fungi belong.

Ericoid mycorrhizal fungi
Fungi in a mycorrhizal symbiosis with certain members of the plant family Ericaceae that is characterized by the penetration of hair root cells and the formation of hyphal coils. Ericoid mycorrhizal fungi include diverse species from the Basidiomycota and Ascomycota phyla.

Biogeographical diversity. Whether fungal diversity exhibits biogeographical patterns is a long-standing debate among mycologists[34,35] (more long standing even than the better known debate about the Baas Becking 'everything is everywhere' hypothesis[36]; BOX 3). Indeed, many major fungal lineages arose sufficiently early and dispersed well enough to have nearly global distributions. For example, most major genera of fungi, such as the ectomycorrhizal genera *Russula*, *Boletus*, *Inocybe*, *Cortinarius* and *Amanita*, seem to be present on all habitable continents[4,37,38]. As with the plant and animal kingdoms, some of the deepest biogeographical splits in the fungal kingdom are between taxa from the Northern and Southern hemispheres, which is

Gondwanan
Arising from Gondwana, the supercontinent that broke up approximately 180 million years ago and included parts of present day South America, Australia, New Zealand and Antarctica.

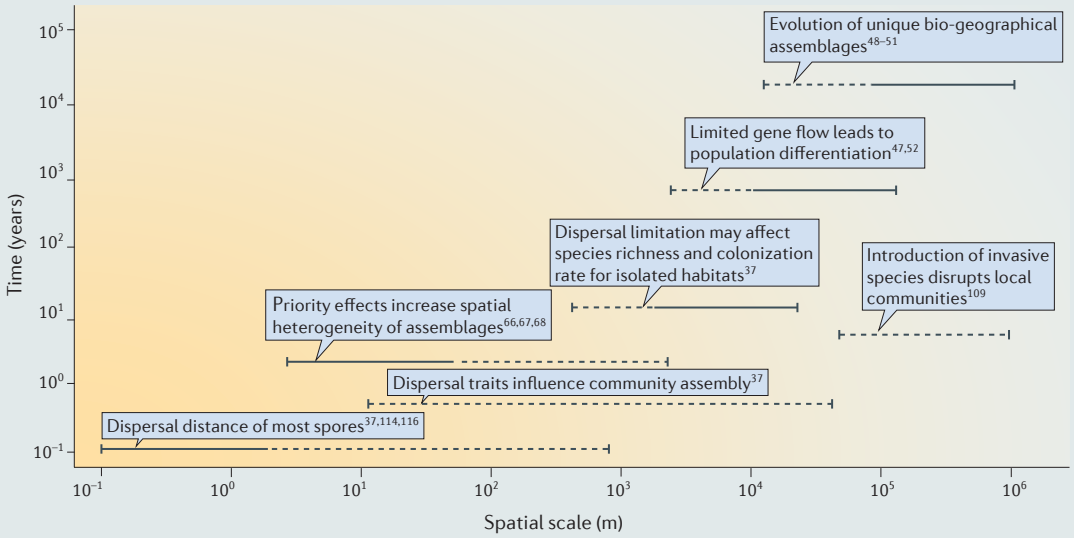
Cosmopolitan
In ecology, a very wide geographical distribution, often across several continents. Cosmopolitan taxa frequently traverse large dispersal barriers, such as oceans or mountains.

Endemism
In ecology, a restricted geographical distribution. Endemism can occur at a range of spatial scales, from a single lake or mountainside, to a continent.

consistent with a divergence that has Gondwanan origins[39]. However, although genera and other higher-level taxa are broadly distributed, it has become increasingly evident in recent years that most fungal species do not generally have cosmopolitan distributions and that patterns of fungal diversity at the species level are strongly influenced by biogeographical factors, such as climate[4] and isolation[3,40]. In fact, regional endemism is one of the most consistent results from sequence-based continental-scale and global-scale studies of fungal communities[41]. This was well demonstrated by an analysis of >52,000 species of fungi — with species defined at approximately 98% internal transcribed spacer (ITS) sequence similarity (BOX 1) — present in public sequence databases, which found that approximately 80% of these species were endemic to a single continent[42]. In addition to continental endemism, patterns of geographical clustering — in which spatially adjacent fungal communities share a larger number of taxa in common than spatially non-adjacent fungal communities — can be observed at local and regional scales.

Although geographically clustered patterns of fungal community similarity are undoubtedly due, in part, to spatial variation in climate and environment, NGS studies also indicate that dispersal has an important role in shaping fungal communities. For example, the results of a study that sequenced fungi from approximately 600 soil samples across North American Pinaceae forests were highly consistent with dispersal limitation (BOX 3), as statistical ordinations showed strong geographical clustering of fungal communities[3], and community similarity decreased with increasing distance between samples, even after controlling for climate and environment. In fact, the geographical signal of fungal communities in soil is so strong that fungal community composition can be used to identify the origin of dust samples[43]. Although fungal communities overall show strong patterns of regional endemism and dispersal limitation, long-distance dispersal can occur over short timescales through the aerial movement of spores or, over longer timescales, alongside the migration of vegetation during climatic change (see below).

Box 3 | **Spore dispersal**



Although hyphae can extend short distances during growth, spores are the primary agent of rapid dispersal for fungi. In fact, the explosive discharge of fungal spores is among the fastest accelerations ever observed in nature[123]. Effective dispersal is a crucial process for most fungi, owing to the lack of contiguity in the temporal and spatial distributions of resources that are required for growth. The difficulty of effective spore dispersal is reflected in the diversity of spores and spore-bearing structures that are produced by fungi[124]. Most fungi produce several types of spores, which can vary in ecological function, sexuality, longevity and dispersal capacity. The mechanisms of spore liberation are also diverse and often involve specialized tissues and structures — such as mushrooms — to hold spores, as well as adaptations to improve wind or water dispersal or to attract animal vectors[124].

Several recent studies have used molecular[50] and mathematical[125] approaches to quantify the spatial scale of fungal dispersal in natural systems. These studies show that the majority of fungal spores move only centimetres to metres. Consequently, the deposition of spores is highly variable in space and time, and strongly reflects the identity of local fungi and environmental conditions[126]. Although fungi are probably better long-distance dispersers than organisms with larger dispersal units, such as seeds[4], transcontinental dispersal of fungal spores seems to occur relatively rarely and often seems to be the result of human activity[127]. This latter pattern contrasts with early predictions that the propagules of fungi[35], and other microorganisms[36], are everywhere and that community composition is determined solely by local environmental conditions that select for subsets of species from this cosmopolitan propagule pool, which is an idea popularly known as the Baas Becking 'everything is everywhere' hypothesis. Instead, dispersal limitation seems to have a crucial role in producing the patterns of fungal diversity and community structure that are observed across a range of spatial (see the figure, solid lines (or, where speculative, dashed lines)) and temporal scales (see the figure, *y*-axis).

For example, frequent transcontinental dispersal has been inferred in arctic fungi[44], which may occur as a result of the exceptionally large changes in climate that are experienced at high latitudes and the adaptive necessity of long-distance dispersal to track favourable climates.

It is possible that greater sampling depth would reveal more sharing of fungal species across continents[45], which would mean that the pattern of endemism is less strong than current data suggest. Alternatively, it may be that the pattern of endemism is even stronger than currently suspected, as common thresholds that are used to define operational taxonomic units (OTUs; BOX 1) may conceal important genetic variation. For example, at 97% ITS similarity (the most commonly used threshold), two species, *Hymenoscyphus albidus* and *Hymenoscyphus fraxineus* (formerly known as *Hymenoscyphus pseudoalbidus*), are combined into a single OTU, even though *H. albidus* is a litter saprotroph whereas *H. fraxineus* is a pathogen that causes dieback in European ash trees[40]. These broad classifications tend to exaggerate the cosmopolitanism of fungal species, whereas finer-scale genetic approaches inevitably break up single cosmopolitan species into many geographically restricted species[46]. For example, a recently published study that shows global cosmopolitanism for arbuscular mycorrhizal fungi[47] may be an artefact of using a highly conserved gene locus. To illustrate the potential of a highly conserved gene locus to produce such an artefact, consider the effect of using an analogous locus to define mammalian species: such a classification would combine humans, most placental mammals and some marsupials into a single species[48]. Similarly, the litter saprotroph *Thelonectria discophora* in the Ascomycota, was, until recently, thought to be a classic example of a cosmopolitan species, being present on every continent except Antarctica. However, multilocus genotyping of a global isolate collection for this 'species' revealed 16 distinct lineages, each of which has a restricted geographical range[49]. Such genetic divergence is perhaps not surprising given that population genetics analyses of fungi have repeatedly shown limited gene flow between continents[46] and, when habitats are not continuous, even at the smaller scale of hundreds of kilometres[50].

Inferences about fungal biogeography from taxonomic surveys of fungal communities have been complemented with phylogeographical analyses of individual lineages, which can reveal the complex details of evolutionary history that underlie patterns of local endemism (FIG. 2). Phylogeographical studies have been able to determine areas of origin[51], reconstruct historical migration routes[52] and estimate the frequency of long-distance (that is, transoceanic) dispersal events[53]. For example, phylogenetic reconstructions for the group known as Caesar's *Amanita* (*Amanita* sect. *Caesarae*) suggest an origin in the African tropics approximately 56 million years ago, followed by a migration north with the expansion of broadleaf forests that occurred during a warming period and, approximately 4–8 million years ago, a migration through Beringia to North America, with a subsequent migration to Central America approximately 2.7 million years ago. Migratory pathways that are associated with the expansion of vegetation have also been reconstructed for other fungal taxa. For example, current patterns of genetic relatedness in the Périgord truffle (*Tuber melanosporum*) seem to mirror patterns of post-glacial revegetation in the French Alps[54] (FIG. 2). Similarly, the ectomycorrhizal fungi that are associated with alder trees (*Alnus* spp.) have patterns of geographical biodiversity that suggest a co-migration with their host from Asia, across the Bering land bridge and down into southern South America[55], with new species evolving along each of these migratory paths.

Whereas the diversity of fungal communities has always been suspected to be high at the local scale (that is, in a handful of soil or a plant leaf), the regional diversity of fungi is much greater than previously suspected, which means that the biogeographical patterns of fungal diversity are also much stronger than suspected[3,4,34]. We suggest that these patterns are best understood in the light of fungal biology — the unique ecological roles of fungi and the modes of fungal dispersal — and the role of dispersal barriers in the evolution of unique fungal species that occur in isolated biogeographical regions.

Macroecology. In plant and animal communities[56,57], the most widely recognized macroecological patterns are perhaps the latitudinal gradients in species richness and the species–area relationship (SAR; that is, the predictable increase in species richness observed with larger sample areas) (FIG. 2). As many factors change with either latitude (such as productivity, rainfall, area and age of the ecosystem) or area (such as habitat diversity and population sizes), determining whether fungi follow similar patterns will be crucial to understanding the general drivers of fungal biodiversity. The examination of fungal latitudinal diversity gradients has revealed somewhat idiosyncratic patterns between different fungal groups. For example, endophytic fungi are hyperdiverse in tropical forests[1], ectomycorrhizal fungi seem to be most diverse at mid-latitudes[4] and fungal communities that are associated with human habitats show a reverse latitudinal gradient[58]. Some of these patterns can be unified by understanding the resource drivers for different functional groups. For example, fungal pathogens often have restricted host ranges[59], which means that their species richness would be expected to increase in the tropics, where there can be as many as 600 tree species per hectare. Thus, it is not surprising that fungal pathogens show the strongest canonical latitudinal diversity gradient of all fungal groups[4]. By contrast, ectomycorrhizal fungi tend to be host generalists[60] and their patterns of richness do not peak in environments with the highest overall number of tree species. Rather, richness is highest in boreal and temperate forests in which host abundance is greatest, owing to the positive effects of habitat area on diversity[61].

Drivers of diversity in habitats

The vast majority of studies of fungal ecology have attempted to elucidate the resources and environmental conditions that control fungal diversity in a single

Saprotroph
An organism that obtains nutrition from dead organic matter.

Arbuscular mycorrhizal fungi
Fungi in arbuscular mycorrhizal symbiosis with a plant host, which is the most common form of mycorrhizal symbiosis and is characterized by fungal hyphae that penetrate plant cell walls, where they form highly branched structures known as arbuscules. Arbuscular mycorrhizal fungi belong to a single monopyhyletic lineage and evolved with the earliest land plants.

Phylogeographical
Pertaining to the patterns of geographical distribution of phylogenetic lineages.

Beringia
An area of land that includes parts of present day Russia and Alaska and that formed a bridge connecting Asia and North America during the lower sea levels of the Pleistocene glacial periods.

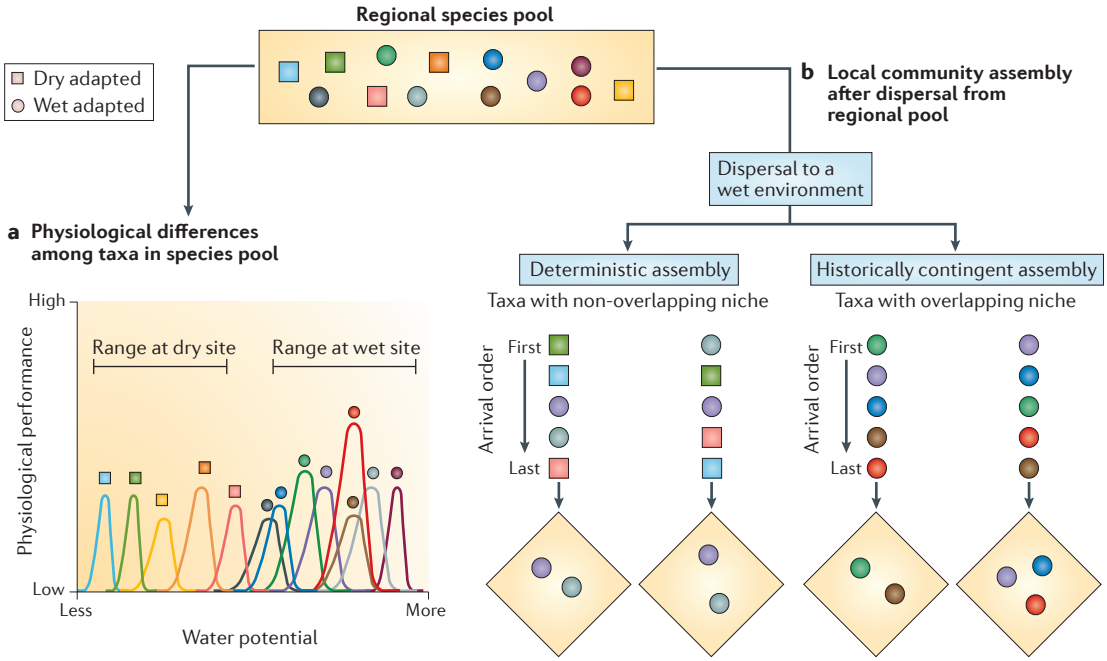


Figure 3 | **Community assembly and historical contingency.** Variation in the taxonomic composition and diversity of fungal communities is shaped by both environmental factors and the effect of chance events. Shown here is a hypothetical set of species, and the different types of community assembly that can occur when a new site is colonized. **a** | The physiological differences between species can be important in determining community assembly at a new site. For example, a set of species that colonize a new site can vary in performance along a gradient of moisture availability, one of the key environmental variables that shapes fungal communities, depending on whether a species is adapted to dry conditions or wet conditions. As in natural systems, wet-adapted species are more numerous than dry-adapted species in the hypothetical set of species shown. **b** | Species disperse at random from the species pool into an environment with wet moisture conditions. In deterministic assembly, the order of arrival of each species does not affect the final composition of the community. Deterministic assembly is likely to occur when there are strong environmental selection pressures and large differences in niche preference between species. By contrast, in historical contingency, the final composition of the community is determined by the order of arrival of each species. Historical contingency occurs when there is strong competition — such as when species have overlapping niche dimensions — and there are strong priority effects in competition.

habitat (BOX 1; Supplementary information S1 (table)). Generalizing across diverse habitats can be challenging, although the availability of moisture seems to be one of the most important environmental conditions that determines the diversity and composition of mycobiomes[62] (FIG. 3). The availability of adequate moisture is crucial for the maintenance of the turgor pressure that is necessary for hyphal extension and for the diffusion and uptake of resources through the cell membrane. For example, a human mycobiome survey found a median of 40–80 fungal genera in the warm, wet conditions that are provided by the human foot[2], but only a median of 2–10 fungal genera on core human body sites such as the back and the forehead. Similarly, in a survey of tropical rainforests, the frequency of samples with culturable fungi from leaf surfaces increased by 50% along a gradient from the sun-rich environment of the upper canopy to the moist environment of the lower tree canopy, and the number of fungal species that were detected increased from 8 to 21 (REF. 63). At larger spatial scales, the diversity of endophytic fungi is highest in tropical rainforests and large studies of soil fungi have found that species richness is positively correlated with climate variables that are related to the availability of moisture, such as annual precipitation and potential evapotranspiration[4,64].

In addition to moisture, nutrient resource availability is a key driver of fungal diversity, and in most ecosystems this is determined by the accessibility and quantity of plant-derived carbon. For example, fungal diversity often decreases with soil depth, owing to the decrease in the availability of organic matter[25]. The lower horizons of the soil are often dominated by a small number of fungal species that are able to access recalcitrant carbon, such as carbon in lignin or tannin, and by mycorrhizal fungi, which are able to access photosynthate from the plant roots[65]. Similarly, the most diverse communities of marine fungi seem to be those in association with corals[31] or sponges[66], which may provide sources of labile carbon. For example, more fungal taxa were reported from deep sequencing of a single coral reef in Samoa[31] (5,410 taxa) than from open sea and the sea bed in a global ocean survey[67] (2,200 taxa). Interestingly, fungal species richness is relatively insensitive to increasing temperature[17,68] or increased levels of atmospheric CO_2 (REF. 69), even in cases in which the composition of fungal communities changes along these gradients.

Evapotranspiration
The sum of evaporation from the surface of the earth and plant transpiration.

One of the most remarkable patterns in studies of fungal (as well as other microbial) communities is the large amount of unexplained variability in diversity and community composition between samples that are taken from the same habitat, such as when comparing individual soil samples, leaves or plant root systems. Although some part of this variation is certainly due to small-scale variation in resources and environmental conditions, an important additional contributing factor is historical contingency in assembly of local communities from regional species pools (FIG. 3). Several studies have demonstrated that when a resource becomes available at a new site, such as a leaf, the first fungus to colonize the site often has a strong competitive advantage and may exclude fungi competing for the same resource that arrive later[70]. When these priority effects are strong, the winner of the competition for resources is determined solely by the order in which taxa disperse to the new site. When dispersal is a stochastic process, the order in which species arrive varies and community composition is contingent on the history of dispersal at each new site. The identity of fungi that arrive early can also influence overall community composition, diversity and function. For example, varying the identity of the first species of wood decomposer fungi to arrive led to changes of up to fivefold in community richness and threefold in community respiration[71]. As the success of dispersal is linked to traits such as spore quality or overall reproductive investment[40], some fungal species have evolved strategies that confer an advantage when competing for the colonization of new sites.

Some evidence suggests that historical contingency may attenuate at larger scales of space, time or community organization. For example, the effects of historical contingency were greater for individual species than for the community-wide characteristics of experimentally assembled communities of wood decomposers, particularly when considering immigration from a larger pool of species[72]. Despite this attenuation, it seems likely that priority effects could operate at large scales, reinforcing biogeographical separation between regions, in terms of both ecology — by increasing the difficulty of local establishment, particularly when only a small number of propagules arrive — and evolution — as most open niches have already been occupied. As such, determining the spatial and temporal extent of historical contingency is an important question for future fungal research.

Other than resource availability, environmental conditions and historical contingency, one other explanation for the seeming lack of predictability of the composition of fungal communities from a given habitat may be related to the spatial distribution of fungal individuals at small scales. Given the relatively large size of fungal individuals, environmental samples may sometimes be too small to adequately represent the community or environment that a species inhabits. As a result, species composition may seem to be highly unpredictable with respect to environmental conditions that are measured at the centimetre scale, but stable and predictable when samples are pooled at the scale of forest stands or tree canopies[73].

Deconstructing functional diversity

Interpreting the biological implications of diversity patterns that are revealed by NGS studies requires knowledge of the key functional attributes of different fungal species. Typically, species are grouped into saprotrophs, mutualists and pathogens, and then each of these trophic groups is divided into functional guilds of species that have different growth strategies and nutrient-acquisition capabilities[73] (FIG. 1). For example, functional guilds of saprotrophs and pathogens may include white rot and brown rot, whereas functional guilds of mutualists may include arbuscular mycorrhizal fungi and ectomycorrhizal fungi. This type of functional information can predict how species will both respond to and affect their environment[13,74]. For example, anthropogenic nitrogen deposition[75] decreases nitrogen limitation and thus the value of ectomycorrhizal fungi, which exchange soil nitrogen for plant photosynthate, to their plant hosts. Consequently, ectomycorrhizal fungi decrease in abundance when traditionally low-nitrogen systems are subject to large inputs of nitrogen. The increasing number of sequenced fungal genomes and studies of extracellular enzyme activity have rapidly improved our ability to determine function from environmental sequencing data[76]. For example, fungi that are plant pathogens often have expanded families of secreted effector proteins, which determine virulence, encoded in their genomes and necrotrophic pathogens often have an increase in the number of genes that encode cell wall-degrading enzymes[77]. However, knowing the key functional features of fungi from the species lists that are generated by sequencing single taxonomic markers, such as ITS, is challenging, as taxonomic assignments are often uncertain[65] and most fungal species have not been cultured. Furthermore, for most fungal species, no data are available for relevant ecological traits such as expression of extracellular enzymes, efficiency of nutrient use, dispersal ability, growth rate or combative ability[62].

For those species that have been cultured, genomic sequencing is revealing substantial variation between species that belong to the same traditional functional guilds, causing a shift away from these classifications towards more continuous, trait-based approaches for understanding fungal activity[13,62]. For example, the classic distinction between white rot and brown rot has been called into question by genetic and biochemical evidence that these fungi fall on a gradient of decay capabilities[78]. Furthermore, not all fungi that are classified as white rot have lignin peroxidases, and species of fungi that are classified as brown rot vary substantially in their ability, and mechanisms used, to break down and take up plant sugars[78,10]. Similarly, certain mutualistic fungi are now known to have the physiological capacity to act as decomposers: many ectomycorrhizal and ericoid mycorrhizal fungi can release extracellular enzymes, break down various plant biopolymers and use the resulting products[79,80]. For example, *Paxillus involutus* releases proteases and several redox-active enzymes, including laccase, tyrosinase, phenylalanine ammonia lyase and enzymes for siderophore metabolism, when exposed to nitrogen resources that require enzymatic breakdown prior to consumption[81].

Historical contingency
When the current state of an ecological community depends on the precise sequence of prior events. Historical contingency is contrasted with determinism, in which a single end state will occur regardless of past events.

Propagules
Any biological unit that is capable of propagating an organism in a new location. For fungi this may include sexual and asexual spores, as well as hyphal fragments.

Forest stands
A contiguous area of forest in which a characteristic species composition and demography enables it to be distinguished from other areas of forest.

Guilds
Groups of species that use similar ecological strategies to exploit a common resource. Species are grouped into guilds irrespective of whether they are taxonomically related.

White rot
Historic classification of certain wood-decomposing fungi. The classification is based on the white colour of the wood that is generated by the enrichment of cellulose that occurs when powerful oxidative enzymes that are produced by these fungi breakdown lignin.

Brown rot
Historic classification of certain wood-decomposing fungi. The classification is based on the brown colour of the wood that is generated by the ability of these fungi to extract polysaccharides while leaving behind lignin.

Various species in ectomycorrhizal genera such as *Suillus*, *Piloderma*, *Cenococcum*, *Amanita*, *Inocybe* and *Russula* can produce large amounts of these and other extracellular enzymes in culture, depending on growth conditions[82–84]. Although ectomycorrhizal fungi typically differ in the levels of extracellular enzymes that they produce compared with free-living saprotrophs, gene expression profiles and laboratory experiments suggest that these plant symbionts have retained the ability of their saprotrophic ancestors to break down complex, recalcitrant forms of carbon in soil to release mineral nutrients, using both traditional white rot mechanisms and, possibly, alternative oxidative mechanisms that are reminiscent of those used by brown rot[80,85,86].

Using a trait-based approach to measure enzyme activity directly will be particularly important if it becomes evident that many taxa do not fit neatly into current notions of functional guilds. For example, endophytic fungi of roots, leaves and stems have historically been considered asymptomatic inhabitants of plants, but recent research is reshaping our understanding of this guild, revealing several benefits of endophytic fungi to the physiology and functioning of plants. Some endophytic fungi have been found to protect plants from pathogens[87], herbivores[88] and challenging environmental conditions[89]. By contrast, other endophytic fungi may facilitate disease in the presence of more virulent pathogens[90]. For example, pre-infection of cottonwood (*Populus* spp.) leaves by some common endophytic fungi, such as *Cladosporium* spp. and *Alternaria* spp., caused up to an 85-fold variation in the severity of rust disease[91]. Similarly, increasing evidence suggests that communities of endophytic fungi contain wood decomposer fungi that are present in a latent state prior to plant death. For example, a quantitative PCR (qPCR) survey of 11 common wood decay fungi found evidence that all of them had latent propagules that were present in living sapwood of a wide range of tree species[92].

Functional classification of fungal communities should increase predictability in fungal ecology studies, as many samples that share few species in common may be quite similar in their functional composition[93]. For example, quantifying the richness and abundance[94] of ectomycorrhizal fungi in soils improves predictions of oxidative enzyme activity[95] and one study found that hyphal morphology changed more consistently than community composition across a large gradient of nutrient availability and water stress in soil[96]. Similarly, the diversity of each trophic group of fungi is driven by a unique set of factors[4]. For example, the diversity of mycorrhizal fungi increases with the relative abundance of host plants, which is probably a proxy for the total size of the habitat or the quantity of resources that are available. In a study of an Amazonian forest in which host plants for ectomycorrhizal fungi were relatively diverse (nine species) but not abundant, only 38 species of these fungi were found[97]. By contrast, in a South American rainforest with host plants that were less diverse (three species) but locally abundant, 120 species of ectomycorrhizal fungi were observed[98]. The effect of resources other than host plants on fungal diversity may be more complicated and depend on the guild in question and competitive interactions with other organisms. For example, decreasing nitrogen availability may increase the species richness of fungi through interactions with both host plants and competitor bacteria by increasing the importance of mycorrhizal associations to tree nutrition and by increasing the competitiveness of decomposer fungi over bacteria. The competitive advantage of these fungi under conditions of low nitrogen may be derived from fungal hyphae, which enable fungi to forage for sparse resources over large spatial areas, and from the generally higher C/N ratios in fungi than in bacteria[99].

Several species from the same functional guild are often observed to coexist in single samples[3,4], which may either be a result of niche partitioning or because competitive exclusion occurs at scales that are smaller than sampling units. To determine which of these possible explanations best accounts for coexistence in functional guilds will require exploration of the traits and activities of the individual fungal species that make up communities at different temporal and spatial scales.

Community structure–function relationships. Studies of whole community function often show that non-overlapping assemblages of species in the same habitat function very similarly, which suggests functional redundancy[3,100,101] (FIG. 4). For example, most soil samples that were taken in a study of North American pine forests shared few fungal taxa in common but often had nearly identical levels of cellulase activity[3]. Functional redundancy is a common structure–function relationship that is observed for taxonomically distinct communities in a single habitat or environment, and probably arises as a result of high local taxonomic diversity and the convergent evolution of common functional guilds. However, in some cases, functional contingency — in which the rates of fungal-mediated processes depends on the composition of the community — can occur instead, as a result of priority effects and historical contingency (see above). In contrast to functional redundancy and functional contingency, which are structure–function relationships that apply to taxonomically distinct communities, the structure–function relationships that can occur between similar communities of fungi are functional plasticity and functional conservatism. Functional plasticity arises when taxonomically similar communities function differently — for example, in response to changing environmental conditions. However, functional conservatism, in which taxonomically similar communities have similar functions, seems to be much more common than functional plasticity in field studies[3,101]. Functional analysis of more fungal communities may shed light on why functional plasticity seems to be a rare outcome and what factors increase the relative importance of each structure–function relationship in fungal communities.

Moving forward, it seems that the functional classification of fungal communities should better predict the rates of fungal-mediated processes than species composition or environmental data alone. In addition, as the study of quantitative traits improves[13,74], it will be increasingly possible to deconstruct aggregated community functions into the individual contributions from different species. Knowing whether there are key taxa or traits that cause

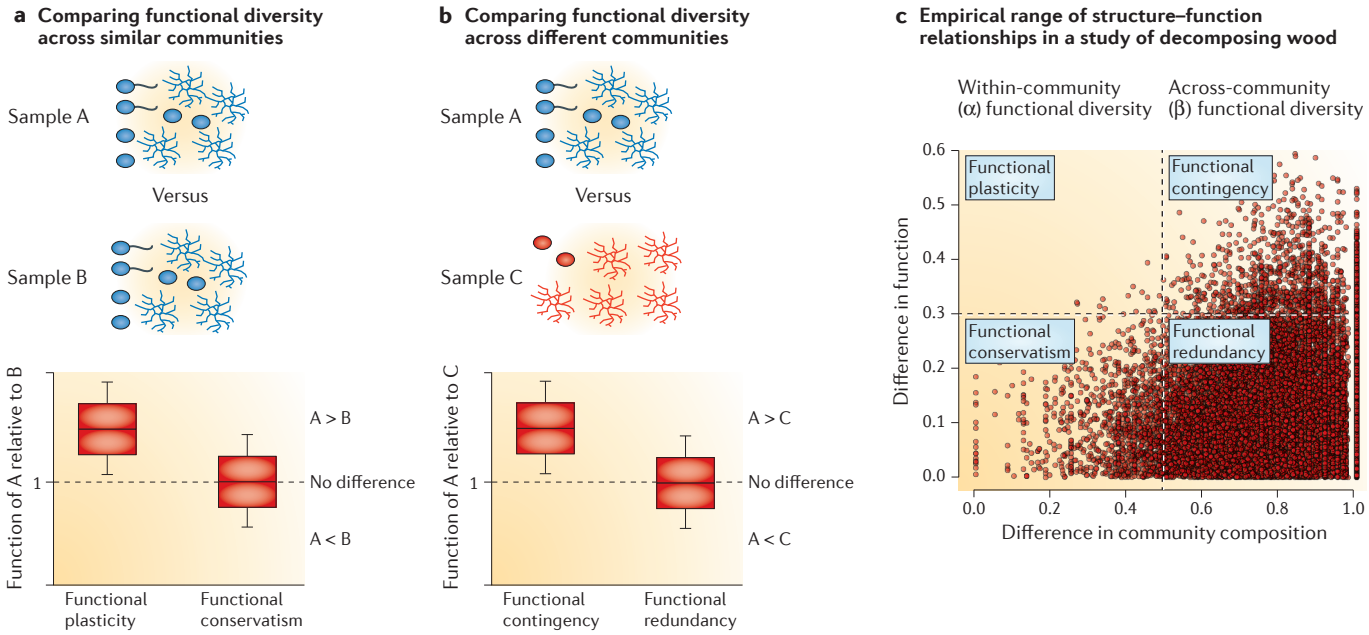


Figure 4 | **Deconstructing structure–function relationships in fungal communities**. Several different structure–function relationships can occur between fungal communities. **a** | Functional plasticity and functional conservatism are structure–function relationships that can occur between taxonomically similar communities. In functional plasticity, communities function differently, despite similar species compositions, whereas functional conservatism describes taxonomically similar communities that also have similar functions. **b** | Functional contingency and functional redundancy are structure–function relationships that can occur between taxonomically dissimilar fungal communities. In functional contingency, the rate of a fungal-mediated process (that is, function) changes in response to community composition, whereas functional redundancy describes communities that function similarly even though they are taxonomically dissimilar. **c** | Structure–function relationships from fungal communities that were sampled from 270 decomposing *Melicytus ramiflorus* branches in New Zealand[101]. Each point represents a pairwise comparison between structure and function in two samples, with structure shown as the difference in community composition (*x*-axis) and function shown as the difference in percentage mass lost during decomposition (*y*-axis). A key area for future research is to understand why particular structure–function relationships are common (such as functional redundancy) and others uncommon (such as functional plasticity). Species-level functional traits should enable a priori predictions of which structure–function relationships exist between communities.

functional contingency, or whether there are instead many ways to build functionally redundant communities, will greatly aid in predicting the rates of those ecosystem processes that are mediated by fungi.

Contrasts with the bacterial microbiome

Fungi are often considered to be a component of the microbiome, but most generalizations about the microbiome are based primarily on observations of bacterial communities[102,103]. This discrepancy is largely due to the lag in large-scale sequencing studies of the mycobiome compared with those of the bacterial component of the microbiome, together with the specialization of most microbiologists in the study of bacteria. Fortunately, as sequencing power has increased, microbial ecologists are more commonly able to simultaneously analyse several taxonomic groups, even lineages as evolutionarily divergent as Bacteria and Fungi. Consequently, it is becoming evident that the diversity patterns and community dynamics of the mycobiome differ from those of the bacterial component of the microbiome in several important respects. For example, compared with bacteria, fungi are more able to tolerate acidic conditions and are less sensitive to changes in pH[100]. Indeed, for bacteria, pH seems to be the single most important driver of community structure in soils at large spatial scales[104], whereas fungi are typically more sensitive to regional climate or other variables[4], although pH can nevertheless constrain both fungal diversity and community structure[47,73]. Similarly, although marked evolutionary divisions seem to exist between communities of marine and terrestrial bacteria[105], marine fungal communities that have been surveyed thus far are not as evolutionarily distinct from their terrestrial counterparts, with many of the dominant marine fungi seeming to be derived from terrestrial lineages of Ascomycota and Basidiomycota[23] (see above) or to occur in both marine and terrestrial environments. For example, 50% of the fungi that were detected in a survey of marine wooden substrata were classified as terrestrial fungi that were facultatively occurring in a marine habitat[106].

In terms of overall diversity, a reconstruction of a comprehensive tree of life found that the domain Bacteria generally seems to be more diverse than the kingdom Fungi[107]. The comparative diversity of bacteria and fungi in terms of species richness in individual communities varies according to habitat, but always seems to be higher for bacteria than for fungi. For example, in soils, species

richness is generally 2–3 times higher for bacteria than for fungi[25], even though the diversity of fungi peaks in this environment. In marine[105] and animal systems[108], fungal diversity seems to decrease by 1–2 orders of magnitude compared with soils, whereas bacterial diversity can remain relatively high. Compared with bacteria, fungi also seem to show greater heterogeneity[25,109] at the local scale and less taxonomic overlap at the global scale[42,110].

Interestingly, even for bacteria and fungi with similar ecologies, some important differences can be observed. For example, different primary factors control both taxon richness and large-scale biogeographical patterns of bacterial and fungal root mutualists (nitrogen-fixing bacteria of the *Frankia alni* species complex and ectomycorrhizal fungi, respectively) that co-occur on alders as host plants[111,112]. Specifically, the species richness of ectomycorrhizal fungi was significantly associated with the concentration of calcium in soil, whereas the community richness of the *F. alni* species complex was not influenced by this or any other soil-related factor. Similarly, biogeographical clustering differed and community composition across sites was not significantly correlated between ectomycorrhizal fungi and the *F. alni* species complex[111,112]. The fact that fungal and bacterial components of the microbiome have different community dynamics may complicate the process of making predictions about the microbiome and the integration of such predictions into the management of animal and plant diseases. However, it reinforces the need for the development of unifying ecological theories that make accurate predictions across different taxonomic groups.

An important caveat to these comparisons of species richness and biogeographical diversity patterns between bacteria and fungi is that the 16S taxonomic marker that is commonly used to study bacterial communities tends to group species together and thus, in contrast with ITS, emphasizes higher-level taxa (that is, genera or families) with broader geographical distributions that probably reflect conserved physiological features (BOX 1). Therefore, it is possible that differences between bacterial and fungal communities would be less pronounced for data that are derived from other taxonomic markers.

Conclusion

Recent studies have revealed a mycobiome that is greater in diversity and complexity than previously imagined. This diversity is highest in soils, in which fungi obtain a large proportion of plant derived carbon, and lowest in marine environments and animals, and arises both from the ability of numerous fungal species to coexist at small scales and from the large degree of turnover in species composition across habitats and spatial scales. Similarly to plants and animals, the species richness of fungal communities exhibits strong biogeographical patterns that are related to climate and to historical connections between landmasses. Dispersal limitation affects fungal diversity at all scales, maintaining regional endemism and influencing local community assembly. At local scales, fungal communities are highly heterogeneous, with large (and often unexplained) differences in diversity and composition across samples from the same site or habitat. This is a result of high functional redundancy and strong historical contingency in fungal communities.

Documenting the patterns of fungal biodiversity has required improvements in molecular tools, but making sense of how fungal diversity interacts with other ecosystem components and processes will require the identification of traits that can disentangle species lists into functional groups or trait values, as well as the identification of the appropriate scale at which we can predict features of the mycobiome. For example, taxonomic composition can be determined by dispersal limitation at continental scales and even at local scales through priority effects. By contrast, functional composition is more deterministic and may be well predicted by local environmental conditions regardless of large-scale geography. Therefore, although the analysis of NGS data has substantial potential for the discovery of diversity, the ability to accurately interpret these data from a functional perspective requires curated databases with genetic data from known organisms as well as some knowledge of the function of sequenced genes and the natural history of the organisms[21,22]. Even the sequencing of functional genes, as opposed to taxonomic markers, using metagenomics or transcriptomics does not always generate data that correlate well with ecological processes, and thus requires contextual knowledge to accurately interpret[22]. Looking forward, maximizing the potential of NGS data to inform the study of functional diversity will require a parallel effort to elucidate the basic biology of fungi through traditional culturing approaches and to sequence individual fungal genomes in conjunction with studies of natural history.

Understanding the fungal dimensions of biodiversity is not solely an academic exercise; it also has direct implications for the welfare of human societies. The rates of globally important processes, such as decomposition of organic matter and nutrient uptake by plants, are determined by fungal community dynamics. Anthropogenic activities that change the composition and richness of fungal communities may fundamentally alter these cycles. Similarly, the deaths of billions of plants and animals that have been caused by fungal pathogens over the past two centuries are largely the product of human economic activity that has enabled these fungi to overcome long-standing biogeographical barriers. Using NGS, we have now scratched the surface of the mycobiome; however, the high level of diversity that has been uncovered by doing so has shown that much more work remains to be done in elucidating the fungal dimensions of biodiversity.

1. Arnold, A. E., Maynard, Z., Gilbert, G. S., Coley, P. D. & Kursar, T. A. Are tropical fungal endophytes hyperdiverse? *Ecol. Lett.* **3**, 267–274 (2000).
2. Findley, K. *et al.* Topographic diversity of fungal and bacterial communities in human skin. *Nature* **498**, 367–370 (2013).
The first in-depth NGS study of the human mycobiome, which demonstrates substantial differences between the distribution of bacteria and fungi.
3. Talbot, J. M. *et al.* Endemism and functional convergence across the North American soil mycobiome. *Proc. Natl Acad. Sci. USA* **111**, 6431–6346 (2014).
This study contrasts regional differences in the composition of fungal species with the convergent production of extracellular enzymes, as evidence for high functional redundancy.

4. Tedersoo, L. *et al.* Global diversity and geography of soil fungi. *Science* **346**, 1256688 (2014).
The first global survey to show strong biogeographical patterns and variable latitudinal diversity gradients in fungi.
5. Pion, M. *et al.* Bacterial farming by the fungus *Morchella crassipes*. *Proc. Biol. Sci.* **280**, 20132242 (2013).
6. Remy, W., Taylor, T. N., Hass, H. & Kerp, H. Four-hundred-million-year-old vesicular arbuscular mycorrhizae. *Proc. Natl Acad. Sci. USA* **91**, 11841–11843 (1994).
7. Floudas, D. *et al.* The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336**, 1715–1719 (2012).
8. Jones, J. D. & Dangl, J. L. The plant immune system. *Nature* **444**, 323–329 (2006).
9. Hohl, T. M., Rivera, A. & Pamer, E. G. Immunity to fungi. *Curr. Opin. Immunol.* **18**, 465–472 (2006).
10. Eastwood, D. C. *et al.* The plant cell wall-decomposing machinery underlies the functional diversity of forest fungi. *Science* **333**, 762–765 (2011).
11. Bagchi, R. *et al.* Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88 (2014).
This paper demonstrates the importance of fungal pathogens in maintaining the diversity of tropical rainforest trees.
12. Taylor, J. W. & Berbee, M. L. Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* **98**, 838–849 (2006).
13. Treseder, K. K. & Lennon, J. T. Fungal traits that drive ecosystem dynamics on land. *Microbiol. Mol. Biol. Rev.* **79**, 243–262 (2015).
A study that identifies key functional traits for fungi and shows how they can be correlated with important ecological processes.
14. Kittelmann, S. *et al.* Simultaneous amplicon sequencing to explore co-occurrence patterns of bacterial, archaeal and eukaryotic microorganisms in rumen microbial communities. *PLoS ONE* **8**, e47879 (2013).
15. Herrera, C. M., Canto, A., Pozo, M. I. & Bazaga, P. Inhospitable sweetness: nectar filtering of pollinator-borne inocula leads to impoverished, phylogenetically clustered yeast communities. *Proc. Biol. Sci.* **277**, 747–754 (2009).
16. Bass, D. *et al.* Yeast forms dominate fungal diversity in the deep oceans. *Proc. Biol. Sci.* **274**, 3069–3077 (2007).
17. Zimmerman, N. B. & Vitousek, P. M. Fungal endophyte communities reflect environmental structuring across a Hawaiin landscape. *Proc. Natl Acad. Sci. USA* **109**, 13022–13027 (2012).
18. Boddy, L. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia* **91**, 13–32 (1999).
19. Smith, M. L., Bruhn, J. N. & Anderson, J. B. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* **356**, 428–431 (1992).
20. Cosgrove, L., McGeechan, P. L., Robson, G. D. & Handley, P. S. Fungal communities associated with degradation of polyester polyurethane in soil. *Appl. Environ. Microbiol.* **73**, 5817–5824 (2007).
21. Peay, K. G. Back to the future: natural history and the way forward in modern fungal ecology. *Fungal Ecol.* **12**, 4–9 (2014).
22. Prosser, J. I. Dispersing misconceptions and identifying opportunities for the use of 'omics' in soil microbial ecology. *Nat. Rev. Microbiol.* **13**, 439–446 (2015).
23. Richards, T. A., Jones, M. D., Leonard, G. & Bass, D. Marine fungi: their ecology and molecular diversity. *Ann. Rev. Mar. Sci.* **4**, 495–522 (2012).
24. Qin, J. *et al.* A human gut microbial gene catalogue established by metagenomic sequencing. *Nature* **464**, 59–65 (2010).
25. Baldrian, P. *et al.* Active and total microbial communities in forest soil are largely different and highly stratified during decomposition. *ISME J.* **6**, 248–258 (2012).
26. Smith, D. & Peay, K. Sequence depth, not PCR replication, improves ecological inference from next-generation DNA sequencing. *PLoS ONE* **9**, e90234 (2014).
27. de Boer, W., Folman, L. B., Summerbell, R. C. & Boddy, L. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiol. Rev.* **29**, 795–811 (2005).
28. Bahram, M., Polme, S., Koljalg, U. & Tedersoo, L. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. *FEMS Microbiol. Ecol.* **75**, 313–320 (2011).
29. Toju, H., Guimaraes, P. R., Olesen, J. M. & Thompson, J. N. Assembly of complex plant–fungus networks. *Nat. Commun.* **5**, 5273 (2014).
30. Jones, M. D. M. *et al.* Discovery of novel intermediate forms redefines the fungal tree of life. *Nature* **474**, 200–203 (2011).
31. Amend, A. S., Barshis, D. J. & Oliver, T. A. Coral-associated marine fungi form novel lineages and heterogeneous assemblages. *ISME J.* **6**, 1291–1301 (2012).
32. Amend, A. S. From dandruff to deep-sea vents: *Malassezia*-like fungi are ecologically hyper-diverse. *PLoS Pathog.* **10**, e1004277 (2014).
33. Ghannoum, M. A. *et al.* Characterization of the oral fungal microbiome (mycobiome) in healthy individuals. *PloS Pathog.* **6**, e1000713 (2010).
34. Bisby, G. R. Geographical distribution of fungi. *Bot. Rev.* **9**, 466–482 (1943).
35. Berkeley, M. J. in *the Gardeners' Chronicle & Agricultural Gazette* (London, 1863).
36. Baas-Becking, L. G. M. *Geobiologie of inleiding tot de milieukunde* (in Dutch) (W. P. van Stockum and Zoon, 1934).
37. Smith, M. E. *et al.* The ectomycorrhizal fungal community in a Neotropical forest dominated by the endemic dipterocarp *Pakaraimaea dipterocarpacea*. *PLoS ONE* **8**, e55160 (2013).
38. Peay, K. G. *et al.* Lack of host specificity leads to independent assortment of dipterocarps and ectomycorrhizal fungi across a soil fertility gradient. *Ecol. Lett.* **18**, 807–816 (2015).
39. Bonito, G. *et al.* Historical biogeography and diversification of truffles in the Tuberaceae and their newly identified southern hemisphere sister lineage. *PLoS ONE* **8**, e52765 (2013).
40. Peay, K. G., Schubert, M. G., Nguyen, N. H. & Bruns, T. D. Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. *Mol. Ecol.* **16**, 4122–4136 (2012).
41. Meiser, A., Balint, M. & Schmitt, I. Meta-analysis of deep-sequenced fungal communities indicates limited taxon sharing between studies and the presence of biogeographic patterns. *New Phytol.* **201**, 623–635 (2014).
42. Kõljalg, U. *et al.* Towards a unified paradigm for sequence-based identification of fungi. *Mol. Ecol.* **22**, 5271–5277 (2013).
43. Grantham, N. S. *et al.* Fungi identify the geographic origin of dust samples. *PLoS ONE* **10**, e0122605 (2015).
44. Geml, J. in *Biogeography of Microscopic Organisms: Is Everything Small Everywhere?* (ed. Fontaneto, D.) (Cambridge Univ. Press, 2011).
45. Gibbons, S. M. *et al.* Evidence for a persistent microbial seedbank throughout the global ocean. *Proc. Natl Acad. Sci. USA* **110**, 4651–4655 (2013).
46. Vincenot, L. *et al.* Extensive gene flow over Europe and possible speciation over Eurasia in the ectomycorrhizal basidiomycete *Laccaria amethystina* complex. *Mol. Ecol.* **21**, 281–299 (2012).
47. Davison, J. *et al.* Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science* **349**, 970–973 (2015).
48. Bruns, T. D. & Taylor, J. W. Comment on "Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism". *Science* **351**, 826–826 (2016).
49. Salgado-Salazar, C., Rossman, A. Y. & Chaverri, P. Not as ubiquitous as we thought: taxonomic crypsis, hidden diversity and cryptic speciation in the cosmopolitan fungus *Thelonectria discophora* (Nectriaceae, Hypocreales, Ascomycota). *PLoS ONE* **8**, e76737 (2013).
50. Branco, S. *et al.* Genetic isolation between two recently diverged populations of a symbiotic fungus. *Mol. Ecol.* **24**, 2747–2758 (2015).
51. Matheny, P. B. *et al.* Out of the Palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *J. Biogeogr.* **36**, 577–592 (2009).
52. Sánchez-Ramírez, S., Tulloss, R. E., Amalfi, M., Moncalvo, J. M. & Carine, M. Palaeotropical origins, boreotropical distribution and increased rates of diversification in a clade of edible ectomycorrhizal mushrooms (*Amanita* section *Caesareae*). *J. Biogeogr.* **42**, 351–363 (2015).
53. Moncalvo, J. M. & Buchanan, P. K. Molecular evidence for long distance dispersal across the Southern Hemisphere in the *Ganoderma applanatum-australe* species complex (Basidiomycota). *Mycol. Res.* **112**, 425–436 (2008).
54. Murat, C. *et al.* Polymorphism at the ribosomal DNA ITS and its relation to postglacial re-colonization routes of the Perigord truffle *Tuber melanosporum*. *New Phytol.* **164**, 401–411 (2004).
55. Kennedy, P. G., Garibay-Orijel, R., Higgins, L. M. & Angeles-Arguiz, R. Ectomycorrhizal fungi in Mexican *Alnus* forests support the host co-migration hypothesis and continental-scale patterns in phylogeography. *Mycorrhiza* **21**, 559–568 (2011).
56. Gaston, K. J. Global patterns in biodiversity. *Nature* **405**, 220–227 (2000).
57. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).
58. Amend, A., Samson, R., Seifert, K. & Bruns, T. Indoor fungal composition is geographically patterned and more diverse in temperate zones than in the tropics. *Proc. Natl Acad. Sci. USA* **107**, 13748–13753 (2010).
59. Gilbert, G. S. & Webb, C. O. Phylogenetic signal in plant pathogen–host range. *Proc. Natl Acad. Sci. USA* **104**, 4979–4983 (2007).
60. Kennedy, P. G., Izzo, A. D. & Bruns, T. D. There is high potential for the formation of common mycorrhizal networks between understorey and canopy trees in a mixed evergreen forest. *J. Ecol.* **91**, 1071–1080 (2003).
61. Peay, K., Kennedy, P., Davies, S., Tan, S. & Bruns, T. Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. *New Phytol.* **185**, 529–542 (2010).
62. Crowther, T. W. *et al.* Untangling the fungal niche: the trait-based approach. *Front. Microbiol.* **5**, 579 (2014).
63. Gilbert, G. S., Reynolds, D. R. & Bethancourt, A. The patchiness of epifoliar fungi in tropical forests: Host range, host abundance, and environment. *Ecology* **88**, 575–581 (2007).
64. Pellissier, L. *et al.* Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps. *Mol. Ecol.* **23**, 4274–4290 (2014).
65. Lindahl, B. D. *et al.* Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytol.* **173**, 611–620 (2007).
66. He, L., Liu, F., Karuppiah, V., Ren, Y. & Li, Z. Comparisons of the fungal and protistan communities among different marine sponge holobionts by pyrosequencing. *Microb. Ecol.* **67**, 951–961 (2014).
67. Tisthammer, K., Cobian, G. M. & Amend, A. S. Global biogeography of marine fungi is shapted by the environment. *Fungal Ecol.* **19**, 39–46 (2016).
68. Coince, A. *et al.* Leaf and root-associated fungal assemblages do not follow similar elevational diversity patterns. *PLoS ONE* **9**, e100668 (2014).
69. Parrent, J. L., Morris, W. F. & Vilgalys, R. CO_2-enrichment and nutrient availability alter ectomycorrhizal fungal communities. *Ecology* **87**, 2278–2287 (2006).
70. Kennedy, P. G. & Bruns, T. D. Priority effects determine the outcome of ectomycorrhizal competition between two *Rhizopogon* species colonizing *Pinus muricata* seedlings. *New Phytol.* **166**, 631–638 (2005).
71. Fukami, T. *et al.* Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecol. Lett.* **13**, 675–684 (2010).
72. Dickie, I. A., Fukami, T., Wilkie, J. P., Allen, R. B. & Buchanan, P. K. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood inhabiting fungi. *Ecol. Lett.* **15**, 133–141 (2012).
73. Sterkenburg, E., Bahr, A., Brandström Durling, M., Clemmensen, K. E. & Lindahl, B. D. Changes in fungal communities along a boreal forest soil fertility gradient. *New Phytol.* **207**, 1145–1158 (2015).
74. Koide, R. T., Fernandez, C. & Malcolm, G. Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytol.* **201**, 433–439 (2014).
75. Lilleskov, E. A., Hobbie, E. A. & Fahey, T. J. Ectomycorrhizal fungal taxa differing in response to nitrogen deposition also differ in pure culture organic nitrogen use and natural abundance of nitrogen isotopes. *New Phytol.* **154**, 219–231 (2002).

76. Kohler, A. *et al.* Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nat. Genet.* **47**, 410–415 (2015).
This paper illustrates the potential of using comparative genomics to identify the key evolutionary pressures and traits that are associated with fungal guilds.
77. Ohm, R. A. *et al.* Diverse lifestyles and strategies of plant pathogenesis encoded in the genomes of eighteen Dothideomycetes fungi. *PLoS Pathog.* **8**, e1003037 (2012).
78. Riley, R. *et al.* Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc. Natl Acad. Sci. USA* **111**, 9923–9928 (2014).
79. Talbot, J. M., Allison, S. D. & Treseder, K. K. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Funct. Ecol.* **22**, 955–963 (2008).
80. Lindahl, B. D. & Tunlid, A. Ectomycorrhizal fungi — potential organic matter decomposers, yet not saprotrophs. *New Phytol.* **205**, 1443–1447 (2015).
81. Rineau, F. *et al.* Carbon availability triggers the decomposition of plant litter and assimilation of nitrogen by an ectomycorrhizal fungus. *ISME J.* **7**, 2010–2022 (2013).
82. Talbot, J. & Treseder, K. Controls over mycorrhizal uptake of organic nitrogen. *Pedobiologia* **53**, 169–179 (2010).
83. Talbot, J. M., Martin, F., Kohler, A., Henrissat, B. & Peay, K. G. Functional guild classification predicts the enzymatic role of fungi in litter and soil biogeochemistry. *Soil Biol. Biochem.* **88**, 441–456 (2015).
84. Burke, D. J., Smemo, K. A. & Hewins, C. R. Ectomycorrhizal fungi isolated from old-growth northern hardwood forest display variability in extracellular enzyme activity in the presence of plant litter. *Soil Biol. Biochem.* **68**, 219–222 (2014).
85. Rineau, F. *et al.* The ectomycorrhizal fungus *Paxillus involutus* converts organic matter in plant litter using a trimmed brown-rot mechanism involving Fenton chemistry. *Environ. Microbiol.* **14**, 1477–1487 (2012).
86. Shah, F. *et al.* Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytol.* **209**, 1705–1719 (2016).
87. Arnold, A. E. *et al.* Fungal endophytes limit pathogen damage in a tropical tree. *Proc. Natl Acad. Sci. USA* **100**, 15649–15654 (2003).
88. Clay, K., Holah, J. & Rudgers, J. A. Herbivores cause a rapid increase in hereditary symbiosis and alter plant community composition. *Proc. Natl Acad. Sci. USA* **102**, 12465–12470 (2005).
89. Marquez, L. M., Redman, R. S., Rodriguez, R. J. & Roossinck, M. J. A virus in a fungus in a plant: three-way symbiosis required for themal tolerance. *Science* **315**, 513–515 (2007).
90. Busby, P. E. *et al.* Leaf endophytes and *Populus* genotype affect severity of damage from the necrotrophic leaf pathogen, *Drepanopeziza populi*. *Ecosphere* **4**, 1–12 (2013).
91. Busby, P. E., Peay, K. G. & Newcombe, G. Common foliar fungi of *Populus trichocarpa* modify *Melampsora* rust disease severity. *New Phytol.* **209**, 1681–1692 (2015).
92. Parfitt, D., Hunt, J., Dockrell, D., Rogers, H. J. & Boddy, L. Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecol.* **3**, 338–346 (2010).
93. Fukami, T., Bezemer, T. M., Mortimer, S. R. & van der Putten, W. H. Species divergence and trait convergence in experimental plant community assembly. *Ecol. Lett.* **8**, 1283–1290 (2005).
94. Bodeker, I. T. *et al.* Ectomycorrhizal *Cortinarius* species participate in enzymatic oxidation of humus in northern forest ecosystems. *New Phytol.* **203**, 245–256 (2014).
95. Talbot, J. M. *et al.* Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. *Soil Biol. Biochem.* **57**, 282–291 (2013).
96. Moeller, H. V., Peay, K. G. & Fukami, T. Ectomycorrhizal fungal traits reflect environmental conditions along a coastal California edaphic gradient. *FEMS Microbiol. Ecol.* **87**, 797–806 (2014).
97. Tedersoo, L., Sadam, A., Zambrano, M., Valencia, R. & Bahram, M. Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. *ISME J.* **4**, 465–471 (2010).
98. Smith, M. E., Henkel, T., Aime, M. C., Fremier, A. K. & Vilgalys, R. Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest. *New Phytol.* **192**, 699–712 (2011).
99. Strickland, M. S. & Rousk, J. Considering fungal:bacterial dominance in soils — methods, controls, and ecosystem implications. *Soil Biol. Biochem.* **42**, 1385–1395 (2010).
100. Rousk, J., Brookes, P. C. & Baath, E. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Appl. Environ. Microbiol.* **75**, 1589–1596 (2009).
101. Peay, K., Dickie, I., Wardle, D., Bellingham, P. & Fukami, T. Rat invasion of islands alters fungal community structure, but not wood decomposition rates. *Oikos* **122**, 258–264 (2012).
102. Hanson, C. A., Fuhrman, J. A., Horner-Devine, M. C. & Martiny, J. B. Beyond biogeographic patterns: processes shaping the microbial landscape. *Nat. Rev. Microbiol.* **10**, 497–506 (2012).
103. Martiny, J. B. H. *et al.* Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.* **4**, 102–112 (2006).
104. Fierer, N. & Jackson, R. B. The diversity and biogeography of soil bacterial communities. *Proc. Natl Acad. Sci. USA* **103**, 626–631 (2006).
105. Lozupone, C. A. & Knight, R. Global patterns in bacterial diversity. *Proc. Natl Acad. Sci. USA* **104**, 11436–11440 (2007).
106. Rama, T. *et al.* Fungi ahoy! Diversity on marine wooden substrata in the high North. *Fungal Ecol.* **8**, 46–58 (2014).
107. Hinchliff, C. E. *et al.* Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl Acad. Sci. USA* **112**, 12764–12769 (2015).
108. Costello, E. K. *et al.* Bacterial community variation in human body habitats across space and time. *Science* **326**, 1694–1697 (2009).
109. Brown, S. P. & Jumponen, A. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. *Mol. Ecol.* **23**, 481–497 (2014).
110. Martiny, J. B. H., Eisen, J. A., Penn, K., Allison, S. D. & Horner-Devine, M. C. Drivers of bacterial β-diversity depend on spatial scale. *Proc. Natl Acad. Sci. USA* **108**, 7850–7854 (2011).
111. Polme, S. *et al.* Biogeography of ectomycorrhizal fungi associated with alders (*Alnus* spp.) in relation to biotic and abiotic variables at the global scale. *New Phytol.* **198**, 1239–1249 (2013).
112. Polme, S., Bahram, M., Koljalg, U. & Tedersoo, L. Global biogeography of *Alnus*-associated *Frankia actinobacteria*. *New Phytol.* **204**, 979–988 (2014).
113. Schoch, C. L. *et al.* Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proc. Natl Acad. Sci. USA* **109**, 6241–6246 (2012).
114. Hawksworth, D. The fungal dimension of biodiversity — magnitude, significance and conservation. *Mycol. Res.* **95**, 641–655 (1991).
115. Taylor, D. L. *et al.* A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitionning. *Ecol. Monographs* **84**, 3–20 (2014).
116. May, R. A fondness for fungi. *Nature* **352**, 475–476 (1991).
117. Prober, S. M. *et al.* Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecol. Lett.* **18**, 85–95 (2015).
118. Fisher, M. C. *et al.* Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186–194 (2012).
119. Cui, L., Morris, A. & Ghedin, E. The human mycobiome in health and disease. *Genome Med.* **5**, 63 (2013).
120. Huffnagle, G. B. & Noverr, M. C. The emerging world of the fungal microbiome. *Trends Microbiol.* **21**, 334–341 (2013).
121. Dowd, S. E. *et al.* Survey of fungi and yeast in polymicrobial infections in chronic wounds. *J. Wound Care* **20**, 40–47 (2011).
122. Nguyen, L. D. N., Viscogliosi, E. & Delhaes, L. The lung mycobiome: an emerging field of the human respiratory microbiome. *Front. Microbiol.* **6**, 89 (2015).
123. Yafetto, L. *et al.* The fastest flights in nature: high speed spore discharge mechanisms among fungi. *PLoS ONE* **3**, e3237 (2008).
124. Ingold, C. T. *Fungal Spores: Their Liberation and Dispersal* (Clarendon, 1971).
125. Norros, V., Penttilä, R., Suominen, M. & Ovaskainen, O. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos* **121**, 961–974 (2012).
126. Peay, K. G. & Bruns, T. D. Spore dispersal of basidiomycete fungi at the landscape scale is driven by stochastic and deterministic processes and generates variability in plant–fungal interactions. *New Phytol.* **204**, 180–191 (2014).
127. Brown, J. K. M. & Hovmoller, M. S. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* **297**, 537–541 (2002).

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