Mopper S, Mitton J, Whitham TG, Cobb NS, Christensen KM. 1991. Genetic differentiation and heterozygosity in pinyon pine associated with herbivory and environmental stress. *Evolution* **45**: 989–999.
Okasha S. 2008. *Evolution and the levels of selection*. Oxford, UK: Oxford University Press.
Parrent JL, Peay K, Arnold AE, Comas LH, Avis P, Tuininga A. 2010. Moving from pattern to process in fungal symbioses: linking functional traits, community ecology, and phylogenetics. *New Phytologist* **185**: 882–886.
Peay KG, Bidartondo MI, Arnold AE. 2010. Not every fungus is everywhere: scaling to the biogeography of fungal–plant interactions across roots, shoots and ecosystems. *New Phytologist* **185**: 878–882.
Rodriguez R, White JF Jr, Arnold AE, Redman RS. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* **182**: 314–330.
Selosse M-A. 2010. Introduction to a Virtual Special Issue on mycoheterotrophy: *New Phytologist* sheds light on non-green plants. *New Phytologist* **185**: 591–593.
Skene M. 1924. *The biology of flowering plants*. London, UK: Sidgwick & Jackson.
Sober E. 1984. *The nature of selection: evolutionary theory in philosophical focus*. Chicago, IL, USA: University of Chicago Press.
Sthultz CM. 2008. *Influence of genes, herbivores and drought on the mortality and ectomycorrhizal fungal community of a foundation tree*. PhD thesis, Northern Arizona University, Northern Arizona, AZ, USA.
Sthultz CM, Gehring CA, Whitham TG. 2009a. Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species. *Global Change Biology* **15**: 1949–1961.
Sthultz CM, Whitham TG, Kennedy K, Deckert R, Gehring CA. 2009b. Genetically-based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. *New Phytologist* **184**: 657–667.
Thompson JN. 2005. *The geographic mosaic of coevolution*. Chicago, IL, USA: University of Chicago Press.
Vacher C, Piou D, Desprez-Loustau M-L. 2008. Architecture of an antagonistic tree/fungus network: the asymmetric influence of past evolutionary history. *PLoS ONE* **3**: e1740.
Whitham TG, Mopper S. 1985. Chronic herbivory: impacts on tree architecture and sex expression of pinyon pine. *Science* **227**: 1089–1091.
Williams GC. 1966. *Adaptation and natural selection*. Princeton, NJ, USA: Princeton University Press.

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Not every fungus is everywhere: scaling to the biogeography of fungal–plant interactions across roots, shoots and ecosystems

Early natural historians viewed the distributions of fungi as independent of ecology, and instead akin to spontaneous generation: if conditions are right, the appropriate fungi will appear (de Candolle, 1820). Accordingly, Miles Joseph Berkeley (1863), the founder of British mycology, writes to Darwin, 'Indeed were not Fungi so much the creatures of peculiar atmospheric conditions, there would seem to be no limit to the diffusion of their species.' Such a perspective captures a view that characterized the early literature in mycology: fungi may appear to have limited geographical distributions, but dispersal *per se* plays no role in determining such distributions. Nearly a century later, Bisby (1943) recognized endemism in fungi but remained convinced that, 'distribution of hosts and substrata primarily controls distribution of fungi'. Whereas appreciation of spatial and historical patterns of biodiversity led Darwin and Wallace to the theory of evolution by natural selection, the perception that fungi are relatively free from dispersal barriers remained influential well into the 20th century (e.g. Bisby, 1943; Raper *et al.*, 1958).

This assumption has been challenged by recent molecular studies of historical biogeography, ecology and population genetics of fungi (Taylor *et al.*, 2006; Lumbsch *et al.*, 2008). Such studies show that although some fungi are capable of long-distance dispersal (Moncalvo & Buchanan, 2008), the distributions of most reflect the same major dispersal barriers (e.g. oceans and mountains) that drive vicariance events in other organisms (James *et al.*, 1999; Matheny *et al.*, 2009). At first glance the dispersal and distribution of fungi may seem like a topic of interest only in an academic sense. However, broad-scale distributions of fungal pathogens, saprotrophs and mutualists influence key ecosystem properties (Fig. 1), which are currently under pressure from anthropogenic change.

The ecological and historical determinants of fungal distributions – particularly those of symbiotic fungi – were a topic of discussion at a special symposium on the phylogenetic and functional patterns of host plants and their associated fungi, as well as several other sessions, at the Botanical and Mycological Societies of America meeting at Snowbird, Utah, in July 2009. Speakers addressed patterns of fungal distributions at scales ranging from experimental gardens to continents, and at levels of biological organization from genotypes to phyla.

Two talks provided ecological evidence that dispersal limitation should be prevalent among fungi: T. E. Galante (SUNY College of Environmental Science and Forestry, USA) and J. L. Stolze-Rybczynski (Miami University, FL, USA) presented statistical and biomechanical models, respectively, based on direct measurements of basidiospore dispersal from fungal reproductive structures, highlighting how structural differences, such as mushroom height, spore shape and size of Buller's drop, determine dispersal distances. These talks also showed that most spores travel only very short distances from their point of origin – for exam-

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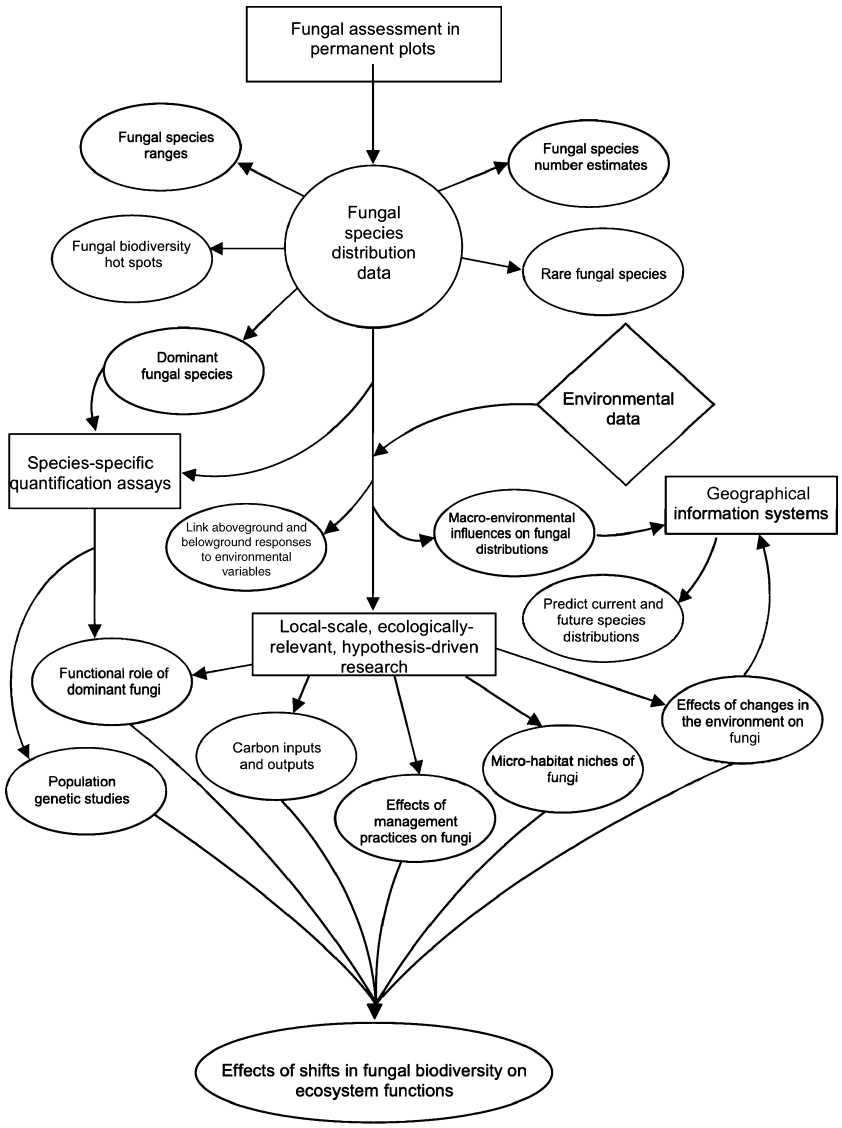

Fig. 1 The potential research outputs of global fungal biodiversity assessments. Rectangles, a research effort; ovals, a research output; diamonds, an instance when data gathered from permanent plots would enhance research efforts.

ple, Galante found that 95% of the spores observed fell within 45 cm of the mushroom from which they originated – and suggest that dispersal limitation may occur even at small to moderate spatial scales. At the community level, differences between species in dispersal strategies can explain patterns of fungal community assembly at landscape scales (Nara, 2009), and isolation and dispersal limitation can lead to significant changes in the species richness and colonization intensity experienced by mycorrhizal host plants (Dickie & Reich, 2005).

At larger spatial and temporal scales, the interplay among dispersal limitation, biogeographical history and adaptive evolution have generated an array of unique fungal assemblages, many of which are just beginning to be characterized by morphological or molecular means. Talks by T. D. Fulgenizi (Humboldt State University, CA, USA) and K. G. Peay (University of California, Berkeley, USA) both described unique ectomycorrhizal communities from the major tropical rainforests of the Amazon and Borneo, respectively. Strong latitudinal changes in fungal community structure were demonstrated for foliar endophytes by A. E. Arnold (University of Arizona, USA), who highlighted the interplay of species diversity and phylogenetic diversity from tropical to arctic environments. A. S. Amend (University of California, Berkeley, USA), presenting a 454 pyrosequencing characterization of indoor environments from every continent, found greater phylogenetic similarity of fungal communities sampled from similar latitudes.

Such latitudinal and biome-level differences in the abundance of particular species, lineages and functional groups are probably linked with ecosystem processes and plant community structure at large spatial scales. For example, the increasing prevalence of ectomycorrhizal symbioses vs arbuscular mycorrhizal symbioses from low to high latitudes and (within tropical forests) from the Amazon to southeast

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Asia (Read, 1991), probably affects regional rates of carbon and nitrogen cycling. Still, relatively little is known about how mycorrhizal type and diversity interact with large-scale soil processes in most of the world.

Understanding determinants of fungal community structure across multiple spatial and temporal scales is particularly important given that fungal communities in a variety of ecosystems have been altered markedly by human activities (e.g. Arnolds, 1991; Lilleskov *et al.*, 2002; Mummey & Rillig, 2006). Since the 1980s, compelling evidence has emerged of a decline in fruiting of forest fungi in northern and central European countries (Arnolds, 1991) and modelling of bioclimatic envelopes predicts changing distributions and possible extinction for some British lichen (Ellis *et al.*, 2007). Some pathogenic and mutualistic fungi are expanding their geographical ranges (James *et al.*, 2009; Pringle *et al.*, 2009), and the phenology of fungi in some forests has changed markedly over the last 50 years, in many cases yielding not one annual fruiting season, but two (Gange *et al.*, 2007; Kauserud *et al.*, 2008). Despite the steady increase in mycological studies from tropical regions, many tropical fungal communities remain unstudied, and the continuing decline in forested areas may lead to a large loss of still uncharacterized biodiversity (Arnold & Lutzoni, 2007).

Moreover, evidence is accumulating that fungal responses to anthropogenic change may have far-reaching consequences. For example, complex changes in rates of fungal decomposition of organic matter have been observed in the context of climate alteration (Lensing & Wise, 2006; Allison & Treseder, 2008). A number of studies indicate that fungal species composition, root and/or shoot biomass, rates of herbivory and susceptibility to pathogens, and rates of nitrogen acquisition and cycling efficiency, respond to environmental changes such as elevated CO_2 (Hunt *et al.*, 2005; Chen *et al.*, 2007; Cudlin *et al.*, 2007; Clark *et al.*, 2009). In turn, these processes will shape large-scale distributions of plants and animals. For example, high specificity has been demonstrated for a number of mycoheterotrophic plants (Bidartondo & Bruns, 2002; Bidartondo, 2005), and experimental tests have shown that the distributions of these plants (many of which are rare or endangered) are constrained by distributions of one or a few species of ectomycorrhizal fungi (Bidartondo & Bruns, 2005; Bidartondo & Read, 2008). Thus, the migration of these plants and others in response to climate change may be constrained by the distribution or co-migration of fungal symbionts. Given that many fungi, as well as plants, differ in their dispersal abilities, it is likely that individual species will differ in the rate of migration in response to global change, which will inevitably lead to the creation of novel communities and interactions (Davis, 1986; Keith *et al.*, 2009). These may lead to temporary disequilibria (i.e. where species are not present in otherwise suitable environments) or to the formation of stable communities of plants and fungi much different from those we see today.

Despite compelling evidence that fungal communities are changing, and that these changes have potential ramifications for key ecosystem properties, we still have little ability to predict or generalize at the spatial and temporal scales necessary to inform sound experimental design for ecology and ecosystem science. This is primarily because we have accurate distributional data for only a small fraction of fungal species and lack the ability to extrapolate functional studies from the laboratory to the ecosystem and from single species to communities. Fortunately, our ability to map large-scale distributions is greater than ever before. From a methodological standpoint, fungal community ecologists have harnessed the power of molecular ecology to permit the following: more holistic and quantitative measures of community structure that take into account uncultured fungi and fungi that fruit infrequently; and rapid analyses at levels of biological organization ranging from genotype diversity to phylogenetic structure (Arnold *et al.*, 2007; Peay *et al.*, 2008). Concurrently, communities of researchers are rallying to enhance the quality and content of databases to accommodate and curate such data (Bruns *et al.*, 2008), and ecologists are calling for use of the baseline distribution data for mycorrhizal fungi, ranging from regional to continental scales and encompassing entire ecosystems (Lilleskov & Parrent, 2007). These efforts will use increasingly powerful next-generation sequencing methods to open up the 'black box' of fungal ecology and to identify and focus on species, lineages or functional groups that are key to providing ecosystem services.

Such a change in perspective will also require scaling from the traits of individual fungi and their individual plant partners, across multiple scales, as well as a clear research framework that identifies links between research efforts and gaps in our knowledge (Fig. 1). With this framework in mind, we propose a series of fundamental questions that we hope will motivate and guide a global fungal biodiversity assessment.

(1) What are the large-scale spatial distributional ranges for fungal species and to what extent are these determined by abiotic and biotic environmental variables vs historical patterns of dispersal and migration?

(2) Can changes in fungal distributions driven by environmental change (i.e. climate shifts, habitat loss and changing host/substrate distribution) be predicted for groups with distinct geographical distributions, and how will this affect the future distribution of symbiotic plants or animals?

(3) Are there ecologically dominant fungi in particular ecosystems? What criteria should we use to identify them? How do they contribute directly to ecosystem processes (such as carbon sequestration) and how much do they indirectly affect ecosystem processes (such as net primary productivity)?

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(4) If there are widespread, dominant fungal species or lineages across biomes and environmental gradients, to what extent are they functionally and genetically homogeneous?
(5) Can data from traditional, small-scale studies be extrapolated directly to entire ecosystems, or are large-scale pilot studies required to account for interactions and non-additive effects in the scaling-up process?
(6) At what spatial scale can we detect key changes in fungal community structure that are related to essential ecosystem functions or responses to perturbations such as climate change? In other words – which scale is appropriate for detecting community responses to disturbance and at which scale do these changes in the fungal community structure translate to changes in ecosystem processes or services?
(7) Where are the geographical hot spots of fungal biodiversity and why?

The increasing interest by the broader ecological community in fungi, the existence of long-term plot networks and the increasing availability of next-generation sequencing technology make a global assessment of fungal diversity a realistically achievable goal now more than ever. We hope that these questions will help to motivate and guide such an effort and believe that the data generated will answer fundamental questions about the distribution and drivers of fungal diversity, provide baseline data for the incorporation of fungi into other ecological study programmes and help to meet the future challenges of global change.

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References

Allison SD, Treseder KK. 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology* **14**: 2898–2909.

Arnold AE, Lutzoni F. 2007. Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* **88**: 541–549.

Arnold AE, Henk DA, Eells RL, Lutzoni F, Vilgalys R. 2007. Diversity and phylogenetic affinities of foliar fungal endophytes in loblolly pine inferred by culturing and environmental PCR. *Mycologia* **99**: 185–206.

Arnolds E. 1991. Decline of ectomycorrhzal fungi in Europe. *Agriculture Ecosystems & Environment* **35**: 209–244.

Berkeley MJ. 1863. *Gardeners' chronicle & agricultural gazette*. London, UK.

Bidartondo MI. 2005. The evolutionary ecology of myco-heterotrophy. *New Phytologist* **167**: 335–352.

Bidartondo MI, Bruns TD. 2002. Fine-level mycorrhizal specificity in the Monotropoideae (Ericaceae): specificity for fungal species groups. *Molecular Ecology* **11**: 557–569.

Bidartondo MI, Bruns TD. 2005. On the origins of extreme mycorrhizal specificity in the Monotropoideae (Ericaceae): performance trade-offs during seed germination and seedling development. *Molecular Ecology* **14**: 1549–1560.

Bidartondo MI, Read DJ. 2008. Fungal specificity bottlenecks during orchid germination and development. *Molecular Ecology* **17**: 3707–3716.

Bisby GR. 1943. Geographical distribution of fungi. *Botanical Review* **9**: 466–482.

Bruns TD, Arnold AE, Hughes KW. 2008. Fungal networks made of humans: UNITE, FESIN, and frontiers in fungal ecology. *New Phytologist* **177**: 586–588.

de Candolle A. 1820. Essai élémentaire de géographie botanique. In: Lomolino MV, Sax DF, Brown JH, eds. *Foundations of biogeography*. Chicago, IL, USA: University of Chicago Press, 28–48.

Chen X, Tu C, Burton MG, Watson DM, Burkey KO, Hu SJ. 2007. Plant nitrogen acquisition and interactions under elevated carbon dioxide: impact of endophytes and mycorrhizae. *Global Change Biology* **13**: 1238–1249.

Clark NM, Rillig MC, Nowak RS. 2009. Arbuscular mycorrhizal fungal abundance in the mojave desert: seasonal dynamics and impacts of elevated co2. *Journal of Arid Environments* **73**: 834–843.

Cudlin P, Kieliszewska-Rojucka B, Rudawska M, Grebenc T, Alberton O, Lehto T, Bakker MR, Borja I, Konopka B, Leski T *et al.* 2007. Fine roots and ectomycorrhizas as indicators of environmental change. *Plant Biosystems* **141**: 406–425.

Davis MB. 1986. Climatic instability, time lags, and community disequilibrium. In: Diamond JM, Case TJ, eds. *Community ecology*. New York, NY, USA: Harper & Roy, 269–284.

Dickie IA, Reich PB. 2005. Ectomycorrhizal fungal communities at forest edges. *Journal of Ecology* **93**: 244–255.

Ellis CJ, Coppins BJ, Dawson TP, Seaward MRD. 2007. Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation* **140**: 217–235.

Gange AC., Gange EG., Sparks TH, Boddy L. 2007. Rapid and recent changes in fungal fruiting patterns. *Science* **316**: 71–71.

Hunt MG, Rasmussen S, Newton PCD, Parsons AJ, Newman JA. 2005. Near-term impacts of elevated CO_2, nitrogen and fungal endophyte-infection on *Lolium perenne* L. Growth, chemical composition and alkaloid production. *Plant, Cell and Environment* **28**: 1345–1354.

James TY, Porter D, Hamrick JL, Vilgalys R. 1999. Evidence for limited intercontinental gene flow in the cosmopolitan mushroom, *Schizophyllum commune*. *Evolution* **53**: 1665–1677.

James TY, Litvintseva AP, Vilgalys RJ, Morgan JAT, Taylor JW, Fisher MC, Berger L, Weldon C, du Preez L, Longcore JE. 2009. Rapid global expansion of the fungal disease chytridiomycosis into declining and healthy amphibian populations. *PLoS Pathog* **5**: e1000458.

Kauserud H, Stige LC, Vik JO, Okland RH, Hoiland K, Stenseth NC. 2008. Mushroom fruiting and climate change. *Proceedings of the National Academy of Sciences USA* **105**: 3811–3814.

Keith SA, Newton AC, Herbert RJH, Morecroft MD, Bealey CE. 2009. Non-analogous community formation in response to climate change. *Journal for Nature Conservation* **17**: 228–235.

Lensing JR, Wise DH. 2006. Impact of changes in rainfall amounts predicted by climate-change models on decomposition in a deciduous forest. *Applied Soil Ecology* **35**: 523–534.

Lilleskov EA, Parrent JL. 2007. Can we develop general predictive models of mycorrhizal fungal community-environment relationships? *New Phytologist* **174**: 250–256.

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Lilleskov EA, Fahey TJ, Horton TR, Lovett GM. 2002. Belowground ectomycorrhizal community change over a nitrogen deposition gradient in Alaska. *Ecology* **83**: 104–115.

Lumbsch HT, Buchanan PK, May TW, Mueller GM. 2008. Phylogeography and biogeography of fungi. *Mycological Research* **112**: 423–424.

Matheny PB, Aime MC, Bougher NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DJ, Soytong K, Trappe JM *et al.* 2009. Out of the palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family inocybaceae. *Journal of Biogeography* **36**: 577–592.

Moncalvo JM, Buchanan PK. 2008. Molecular evidence for long distance dispersal across the southern hemisphere in the *Ganoderma applanatum-australe* species complex (Basidiomycota). *Mycological Research* **112**: 425–436.

Mummey DL, Rillig MC. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. *Plant and Soil* **288**: 81–90.

Nara K. 2009. Spores of ectomycorrhizal fungi: ecological strategies for germination and dormancy. *New Phytologist* **181**: 245–248.

Peay KG, Kennedy PG, Bruns TD. 2008. Fungal community ecology: a hybrid beast with a molecular master. *BioScience* **58**: 799–810.

Pringle A, Adams RI, Cross HB, Bruns TD. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. *Molecular Ecology* **18**: 817–833.

Raper JR, Krongelb GS, Baxter MG. 1958. The number and distribution of incompatibility factors in *Schizophyllum commune. American Naturalist* **92**: 221–232.

Read DJ. 1991. Mycorrhizas in ecosystems. *Experienta* **47**: 376–391.

Taylor JW, Turner E, Townsend JP, Dettman JR, Jacobson D. 2006. Eukaryotic microbes, species recognition and the geographic limitation of species: examples from the kingdom fungi. *Philosophical Transactions of the Royal Society B* **361**: 1947–1963.

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Moving from pattern to process in fungal symbioses: linking functional traits, community ecology and phylogenetics

A growing appreciation of the ubiquity of plant–fungal symbioses and their fundamental importance to plant communities (Smith & Read, 2008; Rodriguez *et al.*, 2009) has led to a recent radiation of research at the ecological intersection of botany and mycology. With new tools helping fungal ecologists frame new questions – and answer long-standing ones with new precision – fungal ecology has entered a transformative phase. As high-throughput and next-generation molecular tools begin to yield unprecedentedly large data sets describing the diversity and composition of fungal communities (e.g. Bidartondo & Gardes, 2005; Jumpponen & Jones, 2009), fungal ecologists are using computational and analytical innovations (e.g. Taylor *et al.*, 2008) to re-cast questions in terms of process, rather than of pattern alone.

A consensus emerged at the 2009 joint annual conference of the Botanical and Mycological Societies of America (Snowbird, UT, USA; http://2009.botanyconference.org) that incorporating functional traits and phylogenetic information into community studies is key to addressing underlying processes – a critical step for moving fungal ecology to a more predictive science. Such a perspective adds to an increasing awareness of the ways that evolution and ecology are linked through functional biology and can be examined at scales ranging from gene expression to broad ecological modes (James *et al.*, 2006; Edwards *et al.*, 2008; Nygren *et al.*, 2008). With a rich history of using molecular approaches for community surveys, an ever-clearer understanding of the fungal tree of life, and a growing wealth of genome sequences, fungal ecologists are poised to examine fungal diversity, functional traits and phylogenetic relationships in novel ways – and to view them through the lens of genomics to characterize, manipulate and conserve fungal 'community symbiomes'.

Characterizing fungal communities using molecular tools

Because many fungal associates of plants are microscopic and/or unculturable, fungal ecologists long have employed molecular tools to characterize fungi in substrates ranging from leaf litter to flower nectar. Such methods have expanded, especially in the last two decades, with high-throughput 454 and Illumina sequencing platforms providing previously unimaginable sampling depth and breadth (e.g. Buee *et al.*, 2009; Jumpponen & Jones, 2009). Although still limited in sequence length and in the degree to which communities can be accurately described (see Avis *et al.*, 2010), such data sets complement culturing, whole-community fingerprinting (e.g. denaturing gradient gel electrophoresis; Bonito *et al.*, 2010), nonsequence-based molecular approaches (e.g. terminal restriction fragment length polymorphism; Dickie & FitzJohn, 2007) and cloning (e.g. Geml *et al.*, 2009) to illuminate fungal diversity.

Presentations at Snowbird showcased not only these approaches but also the progress in bioinformatics tools needed to analyze such data. For example, József Geml and colleagues (University of Alaska Fairbanks, AK, USA) compared sequence data from curated collections of sporocarps of mycorrhizal *Lactarius* to clone libraries from soil, highlighting unexpected spatial partitioning of these fungi in boreal and tundra ecosystems. Ari Jumpponen and colleagues (Kansas State University, KS, USA) used 454 technology to compare the diversity and composition of phyllosphere fungi between rural and nonrural trees, uncovering a striking effect of urbanization on highly diverse fungi associated with healthy foliage.

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