THE FASCINATION OF FUNGI: EXPLORING FUNGAL DIVERSITY

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The 1990s have seen a remarkable resurgence in interest in the variety of Life with which we share the Earth. The Convention on Biological Diversity, drawn up in 1992, has been ratified by 162 Governments and commits them to take action to promote the conservation, sustainable utilization, and the equitable sharing of benefits from biological diversity. *Biodiversity: the UK Action Plan* was issued in 1994, and the first report of the Steering Group appeared last year. Action plans for threatened species and habitats have been prepared, and more are on the way. The plans cover a considerable number of fungi, including lichen-forming species.

Biodiversity, in the sense in which the word is used by the Convention, encompasses the diversity of life at three levels: ecological, organismal and genetic. This paper concentrates on the organismal, taking some of the tracks that have fascinated me in exploring the extent of fungal diversity.

A diversity of Kingdoms

Organismal biodiversity amongst fungi starts at some of the highest levels of classification. For many decades it has been widely acknowledged that fungi were distinct from plants, animals and bacteria but as new ultrastructural and more recently molecular data have been obtained this distinction has become more apparent. Not only is the kingdom *Fungi* well separated from plants; it is closer to the animal than to the plant kingdom. This is perhaps not so surprising as fungi do not manufacture their own food but gain their nutrition from already formed organic molecules as do animals.

A further surprise was that some of the organisms traditionally the domain of the mycologist proved to be quite separate from the kingdom *Fungi*. The oomycetes, i.e. the downy mildews and their allies, prove to be straminopilous algae which have lost their photosynthetic ability, and the enigmatic slime moulds emerge as a remote and particularly ancient group of protozoa.

Molecular data have also confirmed another fact that continues to cause difficulty, or incredulity, amongst some mycologists; that lichens are produced by a range of unrelated fungi. In fact, to be pedantic, the names given to lichens actually refer to the fungal partner of the association. Strictly, the composite lichen structure has no name and it is only the separate fungal, algal or cyanobacterial constituents that do.

How many fungi are there?

By 1988 I had personally described many fungi new to science. These came from a wide variety of habitats and countries; there seemed to be no end to the novelty yet undocumented. I then started to wonder just how many fungi there might really be on Earth. In the 1820s the Swedish father of mycology, Elias Magnus Fries, had forecast that the fungi would prove to be 'the insects of the botanical world', and that mycology would become larger than the rest of botany. Several later mycologists made attempts to estimate the number of fungi and figures in the range 100,000 to 260,000 were published during the years 1943-51.

Inspired by studies in progress by entomologists, I started to accumulate data sets that could be indicative of the extent of species richness. I was particularly interested to obtain information on the numbers of fungi as compared to plants in particular geographic regions, and to the numbers of fungi unique to individual plant species or communities. For example, in the British Isles, there proved to be about six times as many fungi as native plants. In several detailed local studies in the UK, it emerged that fungi outnumbered the plants by 3 - 4 times; at the Slapton Ley National Nature Reserve this figure is already five times and is set towards six.

With several independent data sets converging around the same multiplier, in 1991 I tremulously published the hypothesis that the number of fungi was conservatively 1.5 million; roughly six times the estimated number of vascular plants. The word 'conservatively' is used deliberately as my calculations did not make assumptions about several possible sources of many species, for example ones growing on the millions of undescribed insects in tropical forests. This new estimate attracted considerable interest and I expected data to be presented that would negate the hypothesis. That may yet come, but such hard data as has emerged has been supportive rather than challenging. A few non-mycologists unfamiliar with the extent of host specificity in fungi have felt one million safer, but mycologists have embraced 1.5 million as a reasonable working estimate. If there are 1.5 million species of fungi, how does this compare with the number that are already known? Totalling entries in the 1995 edition of the *Dictionary of the Fungi*, gives a figure of 72,000 (Table 1). The knowledge gap is clearly immense; it implies that we know perhaps as few as 5 % of the fungi on the planet.

Table 1 The numbers of described fungi (modified from Hawksworth et al. 1995).

Kingdom	Phylum	Species
Protozoa		
	Acrasiomycota	12
	Dictyosteliomycota	46
	Myxomycota	719
	Plasmodiophoromycota	45
		812
Chromista		
	Hyphochytriomycota	24
	Labyrinthulomycota	42
	Oomycota	694
		760
Fungi		
	Ascomycota	32,267
	Basidiomycota	22,244
	Chytridiomycota	793
	Zygomycota	1,056
	mitosporic fungi	14,104
		70,464
Total		72,036

Where are the missing fungi?

The question remains as to where the hypothesized remaining 1.43 million unknown fungi are to be found. We need to answer this question for three reasons: (i) to test the hypothesis of species richness; (ii) to identify the habitats most in need of exploration; (iii) to develop bioprospecting strategies for potentially exploitable novel fungi.

The question can be approached from two angles, by either geographical region or habitat. If we consider geographical units first, tropical forests are generally assumed to be richer in biodiversity of all kinds than are boreal or temperate ones. No tropical site has yet been fully inventoried, but in the Guanaste Conservation Area of Costa Rica, the number of fungi to be expected in the planned All-Taxa Biodiversity Inventory (ATBI) has been estimated at around 50,000, of which as many as 35,000 could be new to science.

More tangible tropical examples include the discovery of over 500 fungi in the litter of five tree species in Panama, and 59 (79%) new species of 75 leaf-dwelling ascomycetes collected in one forest in Kenya. In practice, the numbers of fungi discovered in the tropics are directly proportional to the time spent in intensive exploration, 'Smash and grab' quick visits yield fewer novelties as the most widespread and common species will tend to be found first. Rarer species, or ones needing special methods or skills to detect, are less likely to have been found before and so are more likely to be new.

One of the services the International Mycological Institute provides is to catalogue the fungi described throughout the world. This information is published twice-yearly in the *Index of Fungi*. The data are now computerized, enabling us to search to find out how many fungi have been discovered as new in different countries, or found on different hosts. Interestingly, tropical countries were the source of only half (49 %) of the 16,013 new fungi described in the years 1981-90. The top country was the USA with 1623 (10.1%) species, closely followed by India with 1554 (9.7%); the UK total was 459, that is 46 every year. Only 22 countries generated more than 1% to the total. This evidence shows that all countries are imperfectly known mycologically, and that those receiving the most attention from mycologists yield the greatest numbers of novel species.

Unexplored habitats

The number of specialized habitats that have yet to be fully explored for fungi is vast, and even entirely unexpected habitats have come to light within the last 10-15 years. Amongst these are the anaerobic fungi living inside the rumen of herbivorous mammals, and species living inside rock surfaces in the Antarctic. Even plants, traditionally a source of fascinating microscopic fungi, continue to be a major source of new species since few of those which are not economically important have been exhaustively studied. This is illustrated by the pattern of species descriptions from different plant families over the period 1920-90. About three times as many new fungi were described from grasses as from sedges during that 70 year period. That this effect is largely due to intensity of study is evident from the results of research on previously little-researched plants. Looking at two examples; first, the pernicious weed *Lantana camara* has been scrutinized in the search for potential biocontrol agents, and is now known to support 55 fungi, 28 apparently restricted to it. Second, the rush *Juncus roemerianus*, which grows along the US east coast, has been examined by two researchers since 1991; 20 new species have been found from this one species, eight representing new genera.

We are still unclear whether patterns of host specificity seen in temperate areas also apply in the tropics. Several species, sometimes more than one new to science, may be found on the same leaf. But the extent to which other leaves on the same tree also have novel taxa, and whether the same species occur on nearby unrelated trees, is unknown. Critical studies are needed, but some indication can be obtained from an analysis of data from Brazil amassed by Batista and co-workers and compiled for the first time at the International Mycological Institute in 1995. A total of 3340 fungi were associated with 523 plants, an average of 6.4 fungi per plant species on which at least one fungus was found; how many plants were examined without any associated fungi being detected is unknown. Data sets which include all hosts, whether or not any obligate fungi have been found on them will be particularly instructive on this issue. The available data on fungi known from *Eucalyptus* species was also issued from the Institute last year. 1350 species of fungi are known from 150 of the 450-600 known *Eucalyptus* species, although not all trees had been studied. Of the trees with fungi, the number on each host species ranged from 1 through to 282; furthermore, 150 of the fungi on the tree with 282 species were not listed on any other *Eucalyptus*. As a result of analyses of these and other data sets, I proposed at a symposium in Taipei in May 1996 that 5.3 obligate fungi per host plant species was a reasonable working number.

The same pattern to that seen in flowering plants is also encountered in the fungi occurring on other kinds of hosts. Particularly striking has been the realization that lichens are a rich source of novel hitch-hiking fungi. These include obligate pathogens, gall-formers, deformers, commensals, saprobes, and even lichenicolous lichens. The number known has nearly doubled in 20 years, from 457 species in 1976 to 894 by January 1996. These totals are rising exponentially, something illustrated by three studies released in 1996. First, of 53 species of heterobasidiomycetes growing on lichens 46 (92%) were new to science. Second, of 49 species of fissitunicate pyrenomycetes growing on tropical foliicolous lichens, 36 (73%) were new. And third, of 87 fungi now known to grow on species of *Peltigera*, 58 only grow on that one lichen genus. Some of the fungi that grow on lichens can be grown in pure culture and also produce novel secondary metabolites.

Bryophytes, mosses and liverworts, have received less attention from mycologists than the fungi growing on lichens, and can be commended for further study. One study found that 62 (50%) of 123 pyrenomycete fungi found on mosses were new. 52 collections of the single austral moss genus *Dawsonia* yielded 21 ascomycetes new to science. Many thalloid liverworts have fungi living inside them forming mutualistic associations, sharing characteristics with endomycorrhizas.

The largest untapped source of novel fungi, however, is the insects. New data on the extent of host specificity in one predominantly entomogenous group of fungi, the Laboulbeniales which occur mainly on exoskeletons of beetles and flies, has recently been obtained by Alex Weir. He made detailed comparisons based on extensive collections from sites in the UK and Indonesia, on the basis of which he suggests that the actual number of species of this one order is likely to be within the range 10K to 50K; as only 1855 species of the order are already described, this study indicates that only between 3.7% and 18.5% of the species have been named.

The situation may be even worse in the case of trichomycetes, weird and beautiful fungi occurring in profusion in the hindguts of insects. These organisms are so little studied in most regions of the world that generalizations are hazardous, but investigations in recent years by Steve Moss have demonstrated that this is yet another major source of novel fungi.

This survey of habitats yielding unusual fungi would be incomplete without mentioning freshwater and marine situations. The aquatic hyphomycetes with four-armed or sigmoid-shaped spores, first recognized as abundant on decaying leaves and in river foam from studies on a Leicestershire pond by Terence Ingold, are now known from all around the world. The pyrenomycetes with beautifully appendaged ascospores found on wood immersed in sea water, and the seemingly endless new ascomycetes on mangrove pneumatophores, prop-roots and debris, are other examples. Studies by Kevin Hyde in Queensland have also shown that submerged wood in tropical streams is yet another rich source for undescribed pyrenomycetes.

Lost and hidden species

We can also find overlooked species without travelling to exotic regions or striving to find pinkish dots on moss leaves. There are lost, or hidden, species that have already been collected but are not currently recognized. First, named and orphaned species remain 'lost' amongst the 250,000 species names introduced for fungi but are yet to be taken account of in monographic studies. An analysis of 15 fungal monographs showed that each fungus had on average 2.5 names. If this holds across all groups, then 100,000 not 72,000 should be recognized today. This suggests there could be as many as 28,000 fungi remaining in the literature as unadopted 'orphans'.

When genera are revised on a world scale, in some cases the numbers known are reduced significantly where species prove to be plurivorous, for example seven species of *Didymosphaeria* proved to have over 100 synonyms. This is not so in others; of 39 species accepted in *Meliolina* on tropical plants, 26 (67%) were new, and of 20 of *Lichenothelia* on rocks 18 (90%) were undescribed.

Second, most mycologists find it is easier and more exciting to enjoy and collect new fungi in the field than to find the time to formally describe them. This pattern has persisted since the earliest expeditions to remote parts of the globe. Such unnamed material almost invariably comes to rest in folders, drawers, or boxes of specimens awaiting description - sometimes for over a century. Mycologists often pledge themselves to return to their unprocessed collections in retirement, but on finding pastures new each will add his or her unprocessed material to the backlog. The major mycological institutions around the world must each have several thousand putatively new or unexamined pieces of material. I doubt that less than about 20,000 species are awaiting time being found for critical study and description.

Third, some fungi are hidden within described species. In some groups of fungi, there has been a tradition of describing as new species of a genus found on new host plants. This can lead to the unnecessary proliferation of species names, but it can also mask situations where more than one species of a genus occurs on a single host. Many such fungi, on critical examination, can be distinguished and keyed out on morphological criteria with no reference to the host, as in the case of a recent study on *Meliola* in Kenya. The net effect of this is unknown, but experience at IMI suggests that in groups such as *Cercospora* and *Meliola* too few species rather than too many may be currently recognized on some host plants.

There are also cryptic biological species hiding within known species. For example, populations within morphologically defined species are known, separated by a variety of different mechanisms which stop them from interbreeding with other populations. Experimental data are accumulating which suggest that it may be the rule rather than the exception for several functional biological species to either masquerade under a single species name, or be recognized only at an infraspecific rank or as 'special forms'. If a biological species concept were felt to be a must in all cases, something not always supported by what I have termed the 'pragmatic species concept', the number of fungi in some groups would have to be increased by five or more times.

The examples described lead to one answer to the question: where are the missing fungi? That is, they are everywhere, including our own back yards, and especially in previously little explored habitats.

What are the implications of undiscovered biodiversity?

The enormous scale of our ignorance has particularly important implications for mycologists and pathologists working in little-studied countries or habitats. They need to know answers to a variety of questions that are not easily addressed outside a few major institutions even in the UK, thus:

- What is already known?
- What names are correct?
- How do I store information on my collections?
- How do I identify my collections?
- How do I ascertain what is new?
- How do I make my information accessible?

Answers are far from easy because of the long history of a mismatch between the funding of mycology in relation to the myriads of organisms involved. Some biologists argue that molecular approaches will be the key, but this may not be realistic. As about 1800 fungi new to science are described every year, and less than 100 species are sequenced each year, the gap widens rather than contracts. Technological developments, including automated molecular and other biochemical procedures, are unlikely to be of practical value for many years except in certain fungi of medical and agricultural significance.

The recognition of the vast array of undiscovered diversity in fungi around the world provides both an opportunity and a challenge. It is a frontier ripe for exploration. A previously unencountered specimen is always exciting, and often surprising as organisms with hitherto quite unknown features are revealed. The fungi discovered may merit the description of new orders or families, or exhibit intermediate or combinations of characters which question existing groupings.

The possibilities for new discoveries are exhilarating. The unexplored territory, geographic and habitat, is vast and new recruits to the exciting task of discovering the world's fungi are much needed. As we all have back yards, at the very least metaphorically, anyone willing to learn the necessary skills, either professionally or with the freedom only amateurs can really enjoy, can make new and personal contributions to mycological science while delighting in the fascination of fungi. If you are not already involved in this quest, consider how you might contribute to this tremendous voyage of discovery of the true extent of fungal biodiversity into the next millennium.

Further information

The sources of data referred to in this talk can mostly be located through the following works:

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