

The magnitude of fungal diversity: the 1.5 million species estimate revisited*

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The number of known species of fungi is estimated as at least 74 K, but could be as much as 120 K with allowances for ‘orphaned’ species. Yet in 1990 the magnitude of fungal diversity was estimated ‘conservatively’ at 1.5 M species. This figure has been widely accepted as a working hypothesis, but subsequent estimates have ranged from 500 K to 9.9 M and the bases of these suggestions are analyzed. Additional data pertinent to the estimation of the number of fungal species on Earth that has become available since 1990 is discussed. Site inventories demonstrate the need for long-term (20 yr plus) intensive studies to determine the number of species in a site. Fresh data sets on fungus:plant ratios and degrees of host specificity, especially from well-studied hosts in the tropics, are consistent with earlier estimates. The extent of novelty discovered in recent monographic generic revisions and studies of species in particular habitats varies from 0–96%. Allowances for cryptic species, now known to be widespread by incompatibility and molecular studies, could on their own justify an upward revision by a factor of at least five. To enable confidence in any overall estimate to be increased, more detailed studies, especially on particular sites in the tropics, are needed. The consensus of tropical and molecular mycologists in particular is that an increased estimate could be justified. However, it is prudent to retain 1.5 M as the current working hypothesis for the number of fungi on Earth while additional data to test it further accumulates.

INTRODUCTION

In 1990 the magnitude of fungal diversity¹ was estimated ‘conservatively’ at 1.5 M species (Hawksworth 1991). Early in the history of mycology, Fries (1825) had predicted that the fungi would prove to be analogous to the insects in terms of species richness and render mycology larger than the rest of botany; he did not give an overall figure, but from Fries’ later publications it is evident that he was thinking well in excess of 140 K species. The issue was analyzed in more detail by Bisby & Ainsworth (1943) and Martin (1951), primarily in relation to the numbers of fungi recorded on particular plants; they came up with about 100 K and 260 K respectively. The issue was revisited in 1990 because of the burgeoning interest in biodiversity, and the need to ensure that due attention was paid to fungi not only in global but also in national and local biodiversity assessments. The resultant 1.5 M figure has been widely cited and prompted

much discussion and research as to the numbers of fungi that may be present on Earth.

The 1990 estimate was based on extrapolations from several independent data sets: the numbers of fungi *vs* native plants growing in a particular region, on a cross-section of native plants in Great Britain and Ireland, and the numbers of species discovered in a particular alpine community. Some allowances were made for unstudied substrates and to avoid double-counting of anamorphs with known teleomorphs. Examples were given of the extent of novelty discovered in previously little-studied habitats, such as freshwater, lichenicolous, and marine fungi, which were increasing at a rate of 20–49% each decade, and also from genera and regions that had hitherto received little attention.

The 1.5 M figure was considered conservative for four reasons: (1) a modest 270 K figure had been used for the world number of vascular plants; (2) no separate allowance was made for fungi on the vast numbers of insect species postulated – that alone could have raised the figure to 3 M; (3) the ratios of fungi to plants in particular geographic regions did not take account of the scant data on fungi not on plants occurring within them; and (4) the ratios of fungi to plant species could be higher in tropical and polar regions than in temperate ones. The need for more data from the tropics to test the hypothesis was stressed.

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¹ ‘Fungal diversity’ and ‘fungi’ in this contribution, unless otherwise qualified, refer to all organisms traditionally studied by mycologists, regardless of the kingdoms in which some are now classified; i.e. including chromistan fungi, lichen-forming fungi, slime-moulds, and yeasts.

Yet, notwithstanding these caveats, the 1990 estimate has been widely accepted and cited as a working hypothesis – not only by mycologists but in other accounts of, and by commentators on, global biodiversity. However, other estimates published since 1990 have ranged from 500 K to 9.9 M, and new data sets have become available through a welcome resurgence of interest in tropical fungi and also the databasing of existing information. Ødegaard (2000) has revisited estimates of arthropod diversity on Earth, revising them down from Erwin's (1982) 30 M to 4.8 M (range 2.4–10 M) species in the light of new data. In a parallel vein, this contribution endeavours to re-examine the original hypothesis on fungal diversity in the light of other estimates published since that time, and also new information from site inventories, on fungus:plant ratios, host specificity, and the extent of novelty and cryptic species in particular groups.

DESCRIBED SPECIES

The number of accepted fungal species known by 1995, from addition of the figures given in the generic entries of the *Dictionary of the Fungi* (Hawksworth *et al.* 1995), was 72 K, an increase of 3 K from the figure used in 1990. The number of new species described and so far catalogued in the *Index of Fungi* introduced in the five years 1995–1999 is 5269, although data for 1999 is incomplete (P. M. Kirk, pers. comm.). The rate of description of new species in the ten years 1990–99 averaged 1097 species per year, a fall of 11% from the 1980–89 average of 1229² species per year. This reduction may be starting to reflect a world-wide decline in the number of mycologists engaged in describing new species, rather than a shortage of species to be described. For example, in the UK the number of new species described per year has dropped from 46 in the 1980s to 16 in the 1990s, and the number of systematic mycologists (including lichenologists) in post in universities and other institutions fell from 25 in 1990 to 12 in 2000 – and the latter are increasingly required to undertake duties other than taxonomic research.

Hawksworth (1993) noted that about half the newly described fungal species come from the tropics, but that if individual countries are considered, those generating most new species are not exclusively tropical and then included the USA, France and Japan as well as India and Brazil. A comparable study of the data for 1990–99 revealed a shift with 60% discovered in tropical countries *vs* 40% in others, with India now generating most species (*ca* 913³), followed by the USA (*ca* 819), Australia (*ca* 813), China (*ca* 795) and France (*ca* 565) (Hawksworth & Kirk, unpubl.).

The growth in the overall total due to the description of new species is modified by those being reduced to synonyms or which are anamorphs of known species. Assuming the

2.5:1 rate of synonymy found in a series of major monographs (Hawksworth 1992) applies to the 5269 species described from 1995–99, an additional 2107 species should be added to the 'accepted' 72 K total of 1995. This approach provides a current world total of around 74 K known species.⁴

However, the 74 K figure for the number of known species may be an underestimate as species which may be sound, but which are referred to synonymized genera, will not feature in the *Dictionary* total, and entries for many genera where there are no modern revisions may be conservative. Assuming that around 250 K species names exist, and applying the same rate of synonymy, a possible total of about 100 K known species was arrived at by Hawksworth & Rossman (1997). The recent completion of an on-line world catalogue of fungal names (FUNINDEX) has since produced a more accurate figure of about 300 K for the number of species names of fungi (Kirk 2000). Applying the same rate of synonymy to the 300 K figure yields an estimate of 120 K accepted species.

This difference between the suggested numbers of known species will only be conclusively resolved by critical long-term monographic studies over many decades. Prior to the issue of the next edition of the *Dictionary*, it seems prudent to use 74 K as a conservative working figure, but accept that it could approach 120 K were the identities of all 'orphaned' names reassessed.

ESTIMATED SPECIES

May (1991) was sceptical about some aspects of the basis for the 1.5 M figure, notably the lack of data on the extent of novelty being discovered in the tropics, and whether as many host-specific fungi occurred on tropical as opposed to temperate plants. He argued that newly visited sites should be yielding 95% species new to science, and that the patchiness of distributions of plants in tropical forests was likely to lead to fewer species being restricted to them. Conversely, Pascoe (1990)⁵, independently suggested there were at least ten times as many fungi as vascular plants, with particular reference to Australia, but implying 2.7 M world-wide. Similarly, Smith & Waller (1992) considered 1.5 M too low, estimating that there were probably 1 M undescribed fungi on tropical plants alone. In a critical review of estimated species richness amongst all groups of organisms, Hammond (1992) proposed 1 M; he concluded 500 K was a minimum for the fungi, the 1.5 M 'less cautious but well-supported', and adopted 1 M as a compromise. However, in the consensus overview of species numbers of all groups for the extensively peer-reviewed *Global Biodiversity Assessment*, Hammond (1995) accepted the 1.5 M figure and indicated its accuracy as 'moderate'. He noted the general acceptance of the figure by mycologists, and that the figure had not taken account of species associated with large numbers of insects or cryptic species.

Rossman (1994) approached the problem a different way,

² Note that figures extracted for the analysis of newly described fungi included in Hawksworth (1993) are overestimates by about 30% as some new taxa in ranks other than species and new names could not then be easily distinguished in the database; the figures used here have been subjected to a more rigorous search by P. M. Kirk (pers. comm.) to ensure they only include new species.

³ All country figures are approximate as they were produced from rough analyses of the published locations of type specimens catalogued in the *Index of Fungi* database, not all of which are quickly assignable to countries.

⁴ Totals in the just published ninth edition of the *Dictionary* are given as 80 K species, but totals in many entries were not revised for this edition and so that figure has to be treated with caution. They give 75 K as the expected total.

⁵ This paper was not available to me when preparing the 1990 Presidential Address.

Table 1. Major groups of fungi and estimated world species numbers as compiled by Rossman (1994).

Group	Species world-wide
Well-known	
<i>Aphyllphorales s. lat.</i>	20000
Macrolichens	20000
Moderately well-known	
<i>Agaricales s. lat.</i>	80000
Dematiaceous and aquatic hyphomycetes	80000
<i>Uredinales</i>	50000
<i>Hypocreales</i> and <i>Xylariales</i>	50000
<i>Ustilaginales</i>	15000
Gasteromycetes	10000
<i>Erysiphales</i>	10000
Jelly fungi <i>s. lat.</i>	5000
<i>Pezizales</i>	3000
<i>Myxomycetes</i>	1500
<i>Endomycetales</i> (true yeasts)	1000
Poorly known	
Non-dematiaceous hyphomycetes	200000
Coelomycetes	200000
Other perithecioid ascomycetes	100000
<i>Helotiales</i>	70000
Insect-specific fungi	50000
Crustose lichens	20000
<i>Mucorales</i>	20000
<i>Oomycetes</i>	20000
<i>Chytridiomycetes</i>	20000
<i>Endogonales</i> and <i>Glomales</i>	1000
Total	1028500

Data extracted from Rossman (1994), who also provided information on the estimated number of species in the US (56 800 species) and an All Taxon Biodiversity Inventory (ATBI) of a tropical site (39 600 species).

estimating the number of fungi likely to be present by taxonomic group, based on information in the US National Fungus Collection database, the literature, discussions with other mycologists, and personal experience; this led to an overall figure of just over 1 M (Table 1). Dreyfuss & Chapela (1994), however, based on their own experience and other published studies, considered that 1.3 M endophytic fungi alone might await discovery; this view of endophyte diversity in the tropics has been substantiated by later studies. In particular, the leaves of two co-occurring understorey tree species in Panama yielded 418 endophyte morphospecies, 59% of which were represented by single isolates (Arnold *et al.* 2000), only 140 occurring in more than one leaf (Arnold *et al.* 2001). These authors suggested that tropical fungal endophytes might prove to be hyperdiverse, and in consequence the 1.5 M figure to ‘markedly underestimate fungal biodiversity’ (Arnold *et al.* 2000).

Patterns of diversity in non-lichenized fungi, based on the opinions of 29 mycologists, were compiled by Lodge (1995). Overall, diversity was considered to be greatest in the tropics, especially in humid forests on islands, tropical mountain tops, and large tropical forests. Species with restricted geographical ranges appeared to be common in *Agaricales* regardless of whether temperate or tropical regions were considered.

Based on his earlier experience with revising the ascomycete genus *Didymosphaeria*, Aptroot (1997) suggested that the numbers of described species of ascomycetes should perhaps

be reduced by 90%. However, he accepted that as there were about 50 K ascomycete names, that reduction would imply 5 K species ‘which is obviously far too low’. Comparing his results with the estimated species number for *Didymosphaeria* in the *Dictionary of the Fungi* (Hawksworth *et al.* 1995), however, Aptroot concluded that this gave strong support for the estimated 15 K accepted non-lichenized ascomycetes in that work. Aptroot went on to give a ‘tentative estimation’ of 20–40 K non-lichenized and 20–30 K lichenized ascomycetes world-wide; i.e. 40–70 K ascomycetes overall.

However, Aptroot’s (1997) estimate of 20–30 K lichenized ascomycetes appeared high as despite large numbers of newly described species, especially from the tropics, the total summed from the *Dictionary* entries remained at 13.5 K from the 1983 to the 1995 edition; this is explained by newly synonymized species roughly equating those discovered. A re-examination by Sipman & Aptroot (2001) revealed that the number of accepted lichens has remained largely unchanged at around 13.5 K since 1931, a remarkable 70 years. From an analysis of the numbers of new species being found in different lichenized groups, they estimated that about 4 K (25%) of lichen species remained to be discovered and that most would be tropical and Southern Hemisphere. Their revised estimate of 18 K is almost identical to Galloway’s (1992) earlier ‘realistic’ figure of 17 K (‘possibly even to 20 K’) for the world’s lichen-forming fungi, and seems to be a well-based working figure.

An extensive survey of the fungi associated with two species of palms by Fröhlich & Hyde (1999) suggested a fungus:plant ratio of 33:1 (see below); they consequently considered 1.5 M ‘a very conservative estimate of the number of fungal species extant on the planet’. Analyses by Cannon (1997) on another ascomycete group, *Phyllachoraceae* (see below), led him to note that a ‘possible total rather than a formal estimate’ for all fungi could be 9.9 M worldwide. Shivas & Hyde (1997) estimated the number of plant pathogens, most of which are ascomycetes or ascomycete anamorphs, as 270 K; this figure was based on the assumptions that 75% of plant genera are tropical, each plant genus has on average 50 fungal pathogens, a half of those specific to the genus or a closely related one, and comparatively few known fungal pathogens (500) have a wide host range.

In general macromycetes are less host-specific than microfungi, but the numbers in a particular area compared to plants are pertinent to overall extrapolations. Studying macromycetes in pine-oak forests in Mexico, Cifuentes Blanco *et al.* (1997) found that there were 1300 species in an area with 450 plants, a macromycete:plant ratio of about 3.5:1. Assuming a conservative 270 K plants, that implies almost 1 M macromycete species alone world-wide.

Hawksworth & Rossman (1997) addressed the question of where all the undescribed fungi might be. They drew particular attention to evidence for species richness in tropical forests, numbers of new species found in only recently explored habitats, and several categories of lost or hidden species (*viz* cryptic species, or ones included in known species, ones collected but not yet identified, or named but ‘orphaned’ – not revised and reassessed). They estimated that more than 20 000 new species were resting in folders, drawers

Table 2. Published estimates of the extent of fungal diversity to have appeared since 1990.

Author	Estimated species (millions)
Pascoe (1990)	2.7
Hawksworth (1991)	1.5
Hammond (1992)	1
Smith & Waller (1992)	1 (on tropical plants alone)
Hywel-Jones (1993)	1.5 (insect fungi awaiting discovery only)
Rossmann (1994)	1
Dreyfuss & Chapela (1994)	1.3 (endophytes alone)
Hammond (1995)	1.5
Shivas & Hyde (1997)	0.27 (plant pathogens alone)
Aptroot (1997)	0.04–7 (world ascomycetes alone)
Cannon (1997)	9.9
Fröhlich & Hyde (1999)	1.5 + (figure viewed as very conservative)
May (2000)	0.5
Arnold <i>et al.</i> (2000)	1.5 + (figure markedly underestimates fungal diversity)

or boxes⁶ and their overall answer was ‘almost everywhere, including one’s own backyard’.

May (2000) considered Hammond’s (1995) overall estimate for the number of species of all organisms on Earth to be too high, proposing 6.8 M rather than 12.2 M. He adopted a figure of 500 K for the fungi, cautioning about the problems of scaling-up from local to global totals, and considering it ‘more likely that typical fungal species have wider geographic distributions than typical plant species’ – despite detailed studies that show the opposite. Most fungi are linked to particular host plants as parasites or mutualists and therefore have ranges similar to or less than those of their hosts. Restricted distributions are the norm in macromycetes, although there are exceptions, for example, in some gasteromycetes and polypores (Lodge 1995).

Published estimates discussed here are summarized in Table 2.

SITE INVENTORIES

An exhaustive examination of the fungi in a site requires the study of an extremely diverse range of habitats, many of which require different techniques, and also inputs by mycologists with different skills. In the case of a tropical forest, there are at least 31 niches and habitats to survey and this is likely to need 21 specialists (Hawksworth *et al.* 1997). The complexity of the task has been made more evident in the development of detailed protocols to inventory all fungi in the Guanacaste conservation area in Costa Rica; these were costed at US \$31.6 M for this one site (Rossmann *et al.* 1998). No site in the world is yet comprehensively studied for fungi, and so there is still no hard data on the total extent of novelty actually present in any previously unstudied tropical site. Short collecting trips to the tropics regularly generate

some new species, but such ‘smash and grab raids’ mainly catch the commoner fungi (Hawksworth 1993). It is therefore misleading to cite examples of partial studies not yielding high percentages of novelty as evidence that overall estimates are too high.

The problems of completing inventories for fungi on the basis of short-term surveys and visits have long been recognized. Parker-Rhodes (1955), for example, found by comparing records made on five ‘fungus weeks’ at the Flatford Mill Field Centre in Suffolk, UK, that only 25% of the macromycetes present were recorded on any one course. Watling (1995) analyzed records from courses he ran at, and from visits to, the Kindrogen Field Centre in Perthshire, UK, over the 30 years 1964–1993. He found that the number of additional macromycete records started to level off after about six years and then rise more slowly, almost plateauing after 19 years; interestingly, increases accelerated when additional specialists were present. Intensity of study is critical to the completeness of fungal surveys. This is exemplified by the study of Straatsma, Ayer & Egli (2001) who examined an area of 1500 m² in a Swiss forest weekly during the fungal fruiting season for 21 years. They found 71 222 fruit bodies belonging to 408 species. The number of species found in a single year varied from 18 to 194, only eight species were found in all years, 1–74 additional species not found in any previous year were found every additional year, and even in the last year of the survey 19 species fruited for the first time. These results are consistent with the disparity between ectomycorrhizal fruit bodies and the diversity of ectomycorrhizas detected below ground (Yamada & Katsuyu 2001).

While it is unlikely that the total fungal component of a particular site will be inventoried in the foreseeable future, in view of the enormous resources required (see above), long-term studies on particular sites need to be encouraged.

The length of time needed to undertake total fungal inventories, and also the numbers of species to be expected, is also emphasized by experience gained from the two best known sites for fungi in the world: Esher Common (*ca* 400 ha) in Surrey and the Slapton Ley National Nature Reserve (*ca* 200 ha) in Devon, UK, now with around 2.9 K and 2.5 K species recorded respectively (Cannon *et al.* 2001). Both sites have been studied for over 25 years, yet continue to yield further species, particularly when new ecological niches are examined or specialists make visits. Surprisingly for two sites with many similarities and both located in southern England, only about 40% of the species are recorded in both. This suggests that both sites are still far from a complete fungal inventory. Even highly disturbed sites can yield large numbers of species, for instance 2250 in the grounds of the Royal Botanic Gardens Kew, and 850 in the garden of Buckingham Palace (A. Henrici, pers. comm.).

Hawksworth (1991) compared the numbers of fungi and plants in a range of areas and sites in Britain. The Esher and Slapton inventories, however, show that ongoing studies will lead this to increase. For example, the fungus:plant ratio at Slapton is now 5:1 (and rising) rather than the 3:1 it stood at in 1990. As some microhabitats in that site remain not or barely sampled, the prospects are for the ratio to reach and eventually exceed 6:1.

⁶ For example, during breaks while finalizing this contribution in Madrid, I found two undescribed *Polycoccum* species on specimens of *Chondropsis semiviridis* and *Karoowia adhaerens* on loan from The Natural History Museum in London (BM).

The difficulty of inventorying soil fungi in a site remains. Christensen (1989) found that in a sagebrush-grass ecosystem in Wyoming, additional species of fungi continued to be obtained from the soil with each incremental group of isolates made even after 1100 different fungi had been isolated. There is also the issue of species present which may not be obtained by the culture method used. The extent of this last problem has been made clear by Viaud, Pasquier & Brygoo (2000) using molecular techniques. These authors obtained ITS amplifications from 51 cloned samples and 67 fungi isolated from a single soil sample; only one sequence was common to both data sets (closest to *Talaromyces luteus*). This finding has major implications, demonstrating conclusively that neither method alone provides a true indication of the diversity of fungi in soils.

FUNGUS:PLANT RATIOS AND HOST SPECIFICITY

Fungus:plant ratios were one of the key elements in arriving at the 1.5 M figure (Hawksworth 1991). The 6:1 factor which emerged from that analysis concerned the numbers of fungi (including lichens) occurring on all substrata in a given area and not just the fungi present on plants.

Data from the UK was emphasized in the calculation of the 1990 estimate. A consideration of the current situation on numbers of fungi and plants known in the British Isles is therefore pertinent to any revision of the earlier ratio. Additional fungi continue to be added to the UK list. While there is no overall fungal checklist available, the 12 K figure used in the 1990 calculation has been growing each year. On average around 40 species (species new to science and first records in the country) are currently being added to the UK list each year, but new synonymies are also coming to light. Thirty would be a conservative figure for the annual growth in the total, which means that about 300 species of fungi will have been added since 1990. At the same time, the number of native vascular plants in the British Isles has been reassessed (Page 2001, Rich 2001) and now stands at 1461 species (without critical 'microspecies') or 2271 (with critical 'microspecies'). This means that the ratio of the number of fungi to vascular plants in the British Isles lies between 5.4:1 (with critical 'microspecies') and 8.4:1 (without critical 'microspecies'). In arriving at the 6:1 ratio in 1990, a figure of 2089 vascular plants species was employed, *excluding* 'microspecies'. This means that the equivalent ratio of fungi to native vascular plants should be revised upwards to 8.4:1. A simple extrapolation of that ratio to a world scale using the same estimate of 270 K vascular plant species gives an estimate of 2.27 M for the number of fungi on Earth rather than the 1.62 M (neither figure adjusted for double counting of anamorphs with known teleomorphs).

Most subsequent studies have focused on the numbers of fungi actually associated with particular plants rather than on ratios considering fungi in all habitats in a region, with the notable exceptions of the studies of Guzmán (1998) and Rossman *et al.* (1998). The degree to which fungi are specific to particular plant or insect hosts, is nevertheless critical to

the confidence that can be placed on extrapolations to global numbers based on fungus:plant ratios in all habitats in an area.

While restriction to particular species has been emphasized in many discussions of the extent of biodiversity, the degree of host specialization of a fungus can be to, for example, plants of a particular family, genus, or group of species as well as to single species. Specialization at all these levels will contribute to the overall fungus:plant ratios. The extent of specificity can vary even within fungi of the same genus.

Cannon & Hawksworth (1995) analyzed the patterns of description of new fungus species in selected plant families and found that many more species were described from plants of economic importance than ones not recognized as of human interest. For example, over the period 1920–89, 4009 new fungus species were described on grasses compared with 797 on sedges; this difference was of a much greater magnitude than a 53% difference that could be explained by the number of plants in each family (*viz* 7590 grass and 3600 sedge species). Computerized data on the pathogenic fungi on grasses in the USA were analyzed by Clay (1995) who found that on average 767 grass species were infected by 9.8 fungi, the actual number ranging from 387 (on corn) to one (many hosts), although no species were as yet recorded for another 631 grass species known in the country. Clay did not consider saprobic fungi, but these were examined on senescent culms of six grasses in Hong Kong by Wong & Hyde (2001). Over three years they found 215 species of fungi, the diversity indices varying from 3.3 to 8.7; however, while none were specific to grasses, they considered the level of richness to support high estimates of fungal diversity. These two studies indicate the necessity of detailed long-term investigations of plants in different stages of growth and decay for the inventory of fungi on particular hosts.

To illustrate the lack of knowledge in other families, Cannon & Hawksworth (1995) compiled data showing how many new taxa had been found on *Cactaceae* and the effect of one group of US workers on the world total; the number of species described on cacti in North America was taken to 105 compared with 22 in Central and 17 in South America. In seeking sound data on host specificity, it is therefore essential to consider groups which have been relatively well-studied, in at least one region of the world.

Hyde (1996), reviewing extensive work on palm fungi in Queensland, considered that there were about 3 pathogens, 100 endophytes, and 10 saprobes for each palm species. Supposing 25% of the fungi to be restricted to single host species, he calculated that 26 should occur on each palm, a plant:fungus ratio of a staggering 1:26; that implies almost 73 K fungi on palms worldwide of which only 1580 (2.2%) are currently known. Hyde, Fröhlich & Taylor (1997) discovered that as many as 75% of the fungi collected from palms were new to science. The 1:26 ratio was subsequently revised upwards to 1:33 following detailed studies on six palms in Australia and Brunei Darussalam (Fröhlich & Hyde 1999). Specificity appears to be less in the mainly tropical *Pandanaceae*; 150 fungi have been described as new from two of its three genera (MacKenzie & Hyde 1997), but the family has around 900 species. This suggests a fungus:host ratio of only 0.2:1, but the well-studied *Freycinetia banksii* has

about 100 fungi reported from it of which some six are not known on other hosts (McKenzie, Whitton & Hyde 2000); further studies on plants in this family may thus be expected to yield many more obligate species.

Cannon (1997) compared the numbers of species of *Phyllachoraceae* in two relatively well-studied areas for these fungi, the Dominican Republic and Puerto Rico, and then made allowances for differences in various latitudes and the extent of collecting. After making allowances for synonyms, he estimated that the family could have 159 K species worldwide, of which only 1150 were known. However, a three-year study of the group in Australia yielded 87 species of which 17 were new to science (Pearce 2000). While Pearce noted that this suggests Cannon's figures 'are exceptionally high', it does demonstrate that there are many undescribed fungi in the family.

Reviewing data on plant pathogen diversity in the tropics, Shivas & Hyde (1997) concluded that each plant genus could be expected to support around 50 fungi of which half would be host specific and few would have wide host ranges. In the cerrado of Brazil, however, the fungi have been found to be quite host specific, with 1–6.3 per plant species (Dianese, Medeiros & Santos 1997).

To gain further information on the degree of host specificity, Hawksworth (1998) compared a number of different large data sets that had not been available for analysis in 1990. These included databases on organisms in the collections of CABI Bioscience, Brazilian fungi, and fungi recorded on *Eucalyptus* and *Pinus* species, as well as some smaller data sets. The unique fungus:plant species ratios in the data sets examined ranged from 1.6:1 to 186:1, the latter value being for species on *P. sylvestris* (and reduced by two-thirds from 558:1 to allow for fungi possibly able to grow on other species of the genus). The total number of fungi known on *P. sylvestris*, including those able to grow on other species, was 893. *Eucalyptus globosus* had 282 species recorded from it, of which 150 were not known to be present on other species of the genus. Fungi on the cork oak *Quercus suber* have also been analyzed; at least 590 species have been recorded, 286 non-lichenized (Franceschini, Marras & Sechi 1993) and 304 lichenized (Fos 1998). A single recently fallen *Elaeocarpus* tree in Papua-New Guinea yielded 200 ascomycetes (173 lichenized) from collections made by eye and hand-lens, including two new genera and many undescribed species (Aptroot 2001), but the extent to which any may be restricted to the same tree species is obscure in the absence of further sampling. The visible fungi of a tree are only a part of its mycobiota, which includes also mycorrhizal, saprobic, and endophytic species of ascomycete and also other fungal groups. The author suggests this one tree could have as many as 250–300 ascomycete species, taking endophytes into account.

Although numbers of fungi may be much higher on trees than less robust and more ephemeral plants, even some herbaceous plants and shrubs yield perhaps surprising results. For instance, Hawksworth (1998) found that at least 92 fungi occur on *Urtica dioica* of which 17 are probably unique to that species, and 55 on *Lantana camara* of which 28 are confined to it. In the case of *Oryza sativa*, however, only two of the 135 fungi reported from it were restricted to that single plant. The

average of three intermediate data sets gave a fungus:plant ratio of 5.3:1 (range 4.3–6:1; for sources see Hawksworth 1998).

In this connection it is pertinent to note the independent observations of Pirozynski (1972) based on five months of intensive work on the plants and microfungi of the Gombe Stream Reserve in north-eastern Tanzania, which I overlooked in 1990 but later discovered (Hawksworth 1993). Pirozynski wrote that 'preliminary sorting indicates that the species' ratio of microfungi alone to phanerogams is at least 3:1 and may even be as high as 5:1'. Additional allowances for macromycetes, lichen-forming fungi, endophytes, entomogenous fungi, soil fungi, etc. would have taken that figure higher, and conservatively to around 8–10:1 – supporting the view that fungus:plant species ratios are higher in the tropics than in temperate areas where the best studied sites are now just reaching 5:1 (see p. 1425).

There has been some suspicion as to whether minute differences in features such as ascospore dimensions justifies the recognition of separate species occurring on different plant hosts. However, in the case of *Mycosphaerella* species and their anamorphs on *Myrtaceae*, molecular studies confirmed that species separated on such features, ascospore germination patterns, and anamorphs were phylogenetically distinct (Crous *et al.* 2001). It is clearly premature to consider combining such taxa without critical molecular investigations.

Studies on the fungi occurring on *Juncus roemerianus*, a salt-marsh plant on the east coast of North America, have shown the presence of 117 species, 48 of which were new to science; 14 belonged to new genera and one a new family (Kohlmeyer & Volkmann-Kohlmeyer 2001). When never previously investigated tropical plants are examined, new species are almost invariably discovered. For example, in Mauritius, endemic plants are proving to be a rich source of novel fungi (Dulyamode, Cannon & Peerally 2001).

The extent to which endophytic fungi may be host-specific in the tropics has also not yet been resolved. There are indications this could be very high and that these fungi could be a much under-estimated component of fungal diversity (see p. 1424), but differences in methodologies and particularly the characterization of sterile morphospecies make comparisons between studies by different researchers difficult (Arnold *et al.* 2001).

The occurrence of fungi on bryophytes has been reviewed by Döbbeler (1997). He found that while up to 40 ascomycetes could occur on particular moss genera, and some fungi were restricted to particular host species, many have few or no obligate fungi. Overall, he estimated that the number of obligate fungi on bryophytes would prove similar to that of the lichenicolous fungi, then posited as 2000 species. Bryophilous fungi remain poorly studied; for example a single specimen of the foliicolous liverwort *Radula flaccida* from Tanzania yielded seven species, while only four bryophilous ascomycetes were known from the whole of Africa.

The only significant study on host-specificity in relation to insects is that on the *Laboulbeniales* on beetles by Weir & Hammond (1997). European studies suggest a beetle:fungus ratio of 1.68–2:1 or more, and data from Sulawesi a figure in the range 1.1–1.3:1. World-wide, the ratio was found to be

around 2.2:1 for those species able to act as hosts to laboulbeniacean fungi. Assuming a world total of two million beetle species, this implies 30 K fungi of this family on beetles, and perhaps 40 K world-wide including those on other hosts. As roughly 2 K species of *Laboulbeniales* are described, this suggests that only 5% are currently known.

Saprobic species have long been recognized as less host restricted than those on living plant parts, as exemplified for poroid and stereoid fungi in the Santa Rosa National Park in Costa Rica where only three of 32 species found more than three or more times showed signs of host specialization (Lindblad 2000). Gilbert, Ferrer & Carranza (2001) examined the frequency of wood-decay polyporaceous fungi in relation to tree species along five transects on Barro Colorado Island, Panama. They found that the diversity and incidence of these fungi exceeded that of the host trees in this tropical forest (43 fungi *vs* 34 tree species from 23 families), was richest on particular hosts where they were most dense, but little evidence of host specificity in this ecological group emerged in the one wet season studied – 58% of the species only being collected once.

The problems of extrapolations based on host-specificity are not unique to fungi. In the case of insects, Ødegaard (2000) concluded that data generated in recent years did not provide any new data on global species richness because uncertainties remained high and the data sets were still too few. However, entomologists have struggled with a concept of ‘effective specialization’ (May 1990) which inversely weights each species against its number of hosts; that idea remains to be developed for fungi, but is allowed for to some degree in the larger data sets now analyzed (see p. 1427).

EXTENT OF NOVELTY

The proportion of new species discovered in previously unstudied habitats or in revisionary studies on a regional or global level is an incontrovertible indicator of the extent of our ignorance. This varies a great deal from group to group, and depends on the intensity of new collecting and whether the habitat or taxonomic group has been examined critically by earlier mycologists. As a result the proportions of new species found can vary greatly, as indicated in Table 3.

Some studies reveal a level of novelty supporting the hypothesis that 90–95% of the fungi on Earth remain to be described, the percentage depending on whether a 74 K or 120 K figure is used for the known species (see above), but others do not. However, few researchers would consider that their work was based on a comprehensive set of collections of the studied groups or areas.

The studies of E. J. H. Corner are especially indicative; 66% of the macromycete species he reported in the Malaysian region in the period 1950–91 were new (Hawksworth 1993). Yet much novelty remained in the country; Watling (1995) found 214 species of ectomycorrhizal fungi in two states on visits in 1992–94 of which 110 (51%) were new. Hawksworth (1993) drew attention to short-term studies from Cameroon, Malawi and Puerto Rico. In Cameroon, 99 (55%) of 181 ectomycorrhizal taxa collected alongside a single trail were

new (*cfr* Watling 1995). In Malawi, collections made over only 40 h yielded 33 new species (15% of the collections), while in Puerto Rico collections over about nine years suggested about 50% novelty in macromycetes on that island. In the Greater Antilles, 7 of 13 (55%) species of *Hygrocybe* sect. *Firmae* proved to be new to science (Cantrell & Lodge 2001), while 22% of 325 agarics and bolete species collected in the same region since 1995 have been found to be undescribed (Lodge, Baroni & Cantrell 2001).

Hypogeous fungi, including truffles, are relatively well known in the Northern Hemisphere, but have received scant attention elsewhere. In one year, 209 species were discovered in Victoria and New South Wales, Australia, of which 152 (73%) were undescribed, including eight genera new to science (Claridge, Cork & Trappe 2000). In contrast, polypores, especially those involved in wood decay, tend to be rather widely distributed and show limited host-specificity, so rather few new species are found in fresh surveys. For example only 3 (2%) of 150 polypore species found in indigenous vegetation in Zimbabwe were new (Mswaka & Ryvarden 1993), and 6 (3%) of 208 discovered in the Greater Antilles since 1995 (Lodge *et al.* 2001) were new. The situation clearly varies from group to group in macromycete fungi.

The numbers of fungi obligately growing on lichens, lichenicolous fungi, known have risen dramatically in the last two decades (Table 3; Hawksworth & Rossmann 1997), and they are being described at an accelerating rate, currently running at about half that for lichenized species (Sipman 1999). It seems possible that 3–4 K of these fungi exist; i.e. that about 65–75% remain to be discovered and described. The specificity of lichenicolous fungi varies considerably, and in some cases may be focussed on the host genus rather than species. *Peltigera* is especially rich, with 87 fungi known from it, 61 of those not recorded from any other host (Hawksworth & Miądlikowska 1997).

Any tendency to select examples that fit a case has to be guarded against as unscientific, but what does seem clear from many examples, of which Table 3 is a selection, is that the highest proportions of new species are found in either hitherto little-investigated ecological niches, or in the tropics.

Several authors have attempted to estimate the percentage of undescribed species of all groups of fungi to be found in a single site or country. An international group of mycologists, having visited the 120 K ha Guanacaste conservation area in Costa Rica, concluded that 40–50 K species could be expected within it of which it would not be unreasonable to expect 40% to be new (Rossmann *et al.* 1998). Guzmán (1998), with over 50 years experience and knowledge of many fungal groups in Mexico, prepared a critical analysis of the species that might be present in the country. He used three separate approaches: (1) the numbers of fungi obligate on plants with an allowance for saprobes and species associated with insects and other substrata (200 K); (2) extrapolating from the UK total:native plant ratio (100 K); and (3) the number known from the better-studied Veracruz State with reductions to allow for anamorphs, extrapolated to the country, and then reduced by 30% (261 K). He concluded that this indicated a total of as many as 200 K fungi in Mexico, of which only 7 K (3.5%) were currently known.

Table 3. Percentages of new species discovered in selected regional and world studies of different systematic and ecological groups of fungi.

Fungus group	Accepted species	New species	Percentage new	Source
Lichenicolous fungi	849	437	96	New species 1976–96 (Hawksworth & Rossman 1997)
Lichenicolous heterobasidiomycetes	53	46	92	Diederich (1995)
<i>Lichenothelia</i>	20	18	90	Henssen (1987)
<i>Helicogonium</i>	18	15	83	Baral (1999)
Australian truffles	209	152	73	Claridge, Cork & Trappe (2000)
Fissitunicate pyrenomycetes on foliicolous lichens	49	36	73	Matzer (1996)
Kenyan asterines and meliolines	75	53	71	Mibey & Hawksworth (1997)
<i>Meliolina</i>	39	26	67	Hughes (1993)
Malaysian macromycetes	786	517	66	Corner's data (Hawksworth 1993)
Mexican oak-pine macromycetes	1300	835	64	Chapela Blanco <i>et al.</i> (1997)
Marine fungi	444	235	53	New species 1979–99 (Kohlmeyer & Volkmann-Kohlmeyer 1991; Hyde, Sarma & Jones 2000)
Ectomycorrhizal fungi in Malaysia	214	110	51	Watling (1995)
<i>Penicillium</i>	225	75	50	New species 1980–97 (Pitt, Samson & Frisvad 2000)
<i>Phaeocollybia</i> in Mexico	19	9	47	Bandala (cited in Guzmán 1998)
<i>Hypoxylon</i>	113	33	28	Ju & Rogers (1996)
Agarics and boletes in the Greater Antilles	325	72	22	Lodge <i>et al.</i> (2001)
<i>Pseudombrophila</i>	21	4	21	van Brummelen (1995)
<i>Pezicula</i>	26	2	8	Verkley (1999)
Polypores in the Greater Antilles	208	6	3	Lodge <i>et al.</i> (2001)
<i>Didymosphaeria</i>	7	0	0	Aptroot (1995)

CRYPTIC SPECIES

Cryptic species, biological species hidden within existing morphospecies, are proving to be commonplace in fungi. Almost all macromycete 'species' studied prove to have more than one intercompatibility group, and the number can be 20 or more (e.g. Aanen & Kuyper 1999). For example, in the single 'species' *Armillaria mellea* five biological species have been recognized in Europe and ten in North America, most of which have now been given formal names, some also being distinguished by often subtle morphological features (Pegler 2000). There are often gaps between the number of formally named species and that of cryptic species now known in a group. For example, *Rhizoctonia solani* is variously treated as 1 to 4 species, but actually includes 13 anastomosis groups (Roberts 2000).

A parallel situation exists within many 'species' of mitospore fungi, and is well documented amongst plant pathogens. In *Fusarium* there are incompatibility groups even within races and special forms of the same species (e.g. Correll 1991). The taxonomic recognition of intercompatible groups which cannot be recognized by morphological features as species, and also divergent genotypes distinguished only by rDNA sequence data, is currently a matter of debate (Brasier 1997). However, at least in the macromycetes, it has been recommended that the emphasis remains on the morphology and that it be accepted that some 'species' include more than one reproductively isolated group (Petersen & Hughes 1998). Against such a background, the development of a unified species concept in fungi is probably unattainable and the 'pragmatic' species concept is likely to remain the norm (Hawksworth 1996).

In *Fusarium*, some 75 species were accepted in 1990. Ten

years later, the number recognized by molecular methods has risen to over 200, although not all are yet formally named (K. O'Donnell, pers. comm.). The *F. graminearum* group (counting all fusaria that produce trichothecene toxins) comprises about 30 species (*cf.* O'Donnell *et al.* 2000), the *F. solani* complex around 50 (*cf.* O'Donnell 2000), those in the *Gibberella fujikuroi* anamorph complex at least 45 (O'Donnell, Cigelnik & Nirenberg 1998), and many *F. oxysporum* lineages recognized as special forms will merit separate recognition (Baayen *et al.* 2000). As yet more 'species' in the genus are analyzed, it seems certain the number of species known will continue to rise, and that 300 is a reasonable estimate of the number of *Fusarium* species diagnosable by DNA sequence data within the next 20 years (K. O'Donnell, pers. comm.) – a four-fold increase implying that we only knew 25% of the species of this relatively extremely well-studied genus in 1990.

Trichoderma was considered as monotypic by some authors into the 1950s. Cultural studies and links to *Hypocrea* teleomorphs led Rifai (1969) to recognize nine species 'aggregates' that were not further subdivided. Critical cultural and morphological studies, together with some molecular data, led Gams & Bissett (1998) to accept 33 species. But that is only the start of an explosion likely to rival that in *Fusarium* in degree. The *Hypocrea schweinitzii* complex and its *Trichoderma* anamorphs alone has been found to include ten species, of which five needed to be newly described (Samuels *et al.* 1998), and a study of 75 isolates from Russia, Siberia and Himalaya using molecular methods revealed five species which appear to be undescribed (Kulling, Szakacs & Kubicek 2000).

Two species of *Letharia* have been traditionally recognized in North America, but the molecular phylogeny reveals six

cryptic species with different reproductive strategies not obviously related to differences in distribution, chemical products, or morphology (Kroken & Taylor 2001).

Leveillula taurica, considered a broad-spectrum powdery mildew, has been found to be a species complex. Material from 21 host plant families referred to this one species has been found by analysis of the rDNA ITS sequence data to be a complex of at least eight species, also with differences in the shapes of the conidia (Khodaparast, Takamatsu & Hedjaroude 2001).

While some of these examples are dramatic, the extent to which cryptic species occur varies from group to group. In some cases morphological separations are confirmed with no discrepancies, as in *Collybia s. str.* (Hughes *et al.* 2001), and in others are found to be linked to small hitherto unemphasized morphological differences as in several lichens now recognized as distinct species (Grube & Kroken 2000). Interestingly, in some cases, for example, *Ramalina culbersoniana*, the gene trees do not always mesh with different chemotypes (LaGrecia 1999).

In order to allow for unnamed cryptic species, Hawksworth & Rossman (1997) suggested multiplying the species numbers by a conservative five in groups where this phenomenon was known to occur. The macromycetes constitute about 19% (13.8 K species of *Basidiomycetes*; Hawksworth *et al.* 1995) and plant pathogens 32% (23 K species; Shivas & Hyde 1997) of existing fungi. If similar proportions were reflected in the 1.5 M total, and subtracting the known species, that would mean adding 1.35 and 2.28 million respectively to the overall estimate – making a staggering 5.1 M.

IMPROVING THE ESTIMATE

In order to provide estimates in which we can have more than the ‘moderate’ confidence than is accorded to the 1.5 M figure for the number of species of fungi on Earth (Hammond 1995), more detailed information is needed on particular sites, fungus:plant, and fungus:insect ratios. While these data are growing, this is unlikely to be sufficient to change materially current estimates. Sustained increased attention to the fungi associated with particular plants or groups of insects, especially in the tropics, is needed.

In view of the long-term nature of the investigations needed to increase confidence in extrapolated estimates, surrogates indicative of the overall richness of sites need to be considered (Cannon 1997, Hawksworth *et al.* 1997). Selected groups and hosts have been proposed for rapid biodiversity assessments: macromycetes, *Xylariaceae*, lichen-forming fungi, endophytes, palms, bamboo, pandans, freshwater fungi, and pathogens (Hyde *et al.* 2000). However, to use such surrogates to estimate total species richness in a site, their relationship to a complete inventory of all fungi present in a locality needs to be determined.

CONCLUSIONS

There were huge confidence margins in reaching the estimate of 1.5 M species in 1990 (Hawksworth 1991). It is therefore appropriate to re-examine whether that figure should be retained as a working hypothesis in the light of the data which

has become available in the last ten years. A working figure for general use must be based on the best data available, and is there to be tested. However, as in the case of generalist classifications, such figures for general consumption should not be changed until the evidence is overwhelming.

The available evidence suggests that fungal diversity in the tropics is greater than in temperate regions (Fröhlich & Hyde 1999, Lodge 1995), and that little studied genera and ecological niches generate levels of novelty not discordant with our knowing only about 5% of the fungi on Earth (Table 3). Further, the revised fungus:native vascular plant ratio in the British Isles has been revised upwards suggesting that the unadjusted extrapolation to 1.6 M based on that data set was too low. Results of recent data generated by almost all mycologists working in the tropics, or at the molecular level, is also that, if anything, the estimate of 1.5 M is too low.

Notwithstanding these independent data sets all suggesting an upward revision of the 1.5 M figure, I consider that it would be prudent to retain and not increase that number until a consensus on a new working figure based on fresh and independent data sets emerges.

While the jury is still out, and likely to be so for many years considering the still too limited attention given to fungi worldwide, the debate and new research which followed the 1990 estimate has served to engender a new awareness of the richness of fungi amongst ecologists and conservationists – as well as mycologists.

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