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An estimate of the lower limit of global fungal diversity

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Abstract We conservatively estimate that there is a minimum of 712,000 extant fungal species worldwide, but we recognize that the actual species richness is likely much higher. This estimate was calculated from the ratio of fungal species to plant species for various ecologically defined groups of fungi in well-studied regions, along with data on each groups' level of endemism. These calculations were based on information presented in the detailed treatments of the various fungal groups published in this special issue. Our intention was to establish a lower boundary for the number of fungal species worldwide that can be revised upward as more information becomes available. Establishing a lower boundary for fungal diversity is important as current estimates vary widely, hindering the ability to include fungi in discussions of ecology, biodiversity and conservation. Problems inherent in making these estimates, and the impact that additional data on fungal and plant species diversity will have on these estimates are discussed.

Keywords Species diversity · Ratio data · Surrogates

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Introduction

Determining the magnitude and patterns of fungal species diversity has been an ongoing challenge for mycologists (Hawksworth 1991, 2001, 2004; Hawksworth and Rossman 1997; Hyde 2001; Hawksworth and Mueller 2005). Fungi are poorly known, and often ephemeral and cryptic, which makes them difficult to inventory (Mueller et al. 2004). Despite these difficulties, fungi are known to be extremely diverse. Fungi play key roles in ecosystems as decomposers, mutualists, and pathogens, but in most cases the role of individual fungi in nature is unknown. Aside from these roles, fungi have additional economic importance as biocontrol agents and as chemical producers for the pharmaceutical and other industries. Without an estimate of fungal diversity it is difficult to determine the level of redundancy in ecosystem functions provided by fungi. The economic impact of fungi, both positive and negative, is likely related to the total fungal species pool. Ecologists have long sought to explain geographical and other patterns of species diversity, but without information on fungi and other hyper-speciose taxonomic groups it is difficult to judge these explanations. Thus, it would be useful to have some means to estimate total fungal species richness using a relatively easily measured indicator.

Fungi are not the only taxonomic group that is extremely diverse yet poorly studied. Many invertebrate and microbial groups are known to have high species diversity, but, like fungi, most species of these groups are not yet described. To improve our understanding of these extremely diverse groups, ecologists have explored using the species diversity of well known taxonomic groups as surrogates for the species diversity of poorly studied groups (Sisk et al. 1994; Flather et al. 1997). In practice this methodology has had mixed results. Data on regional diversity of butterflies and tiger beetles have been used to predict bird diversity in North America, India, and Australia (Pearson and Carroll 1998), and Lepidoptera diversity was used to predict Hymenoptera species diversity in Ontario (Kerr et al. 2000). However, no correlation was found between the species diversity of moths, butterflies, and birds in forest reserves in Uganda (Howard et al. 1998), and there is little overlap among sites that are species rich in butterflies, dragonflies, liverworts, aquatic plants, and breeding birds in Britain (Prendergast et al. 1993).

It has been suggested that the species diversity of fungi can be estimated using the species diversity of vascular plants in the same region (Hawksworth 1991). This technique has also been used by Pirozynski (1972) in Africa. In small nature preserves with ongoing fungal surveys, there is a high ratio of fungi to plants, and the overlap between similar, extremely well studied preserves is low (Hawksworth 1991; Cannon et al. 2001). We know of only one published statistical test of the efficacy of using plant diversity to predict fungal diversity. Schmit and colleagues (2005) documented that tree species diversity was a statistically significant predictor of macrofungal species diversity through a meta-analysis of plot-based diversity studies in which plant and macrofungal diversity data were provided. Their findings support the use of plants as a surrogate taxon for at least some groups of fungi.

In this paper, we calculate a conservative estimate of the number of extant fungal species worldwide. We combined data on the diversity and geographic distribution of macrofungi, microfungi on plant material, lichenized fungi, aquatic fungi, and soil-inhabiting fungi compiled and presented by the authors of the other papers in this series (Mueller et al. 2006; Hyde et al. 2006; Feuerer 2006; Shearer et al. 2006;

Gams 2006) plus published and unpublished data on arthropod-associated fungi, lichenicolous fungi, and microsporidians to estimate a minimum ratio for the number of fungi to plants for different regions of the world. We then used that ratio, coupled with data on fungal endemism, to determine a lower limit to total fungal species diversity.

Obviously, a great deal of uncertainty is associated with such estimates, and the assumptions used at each stage greatly impacted the final outcome. In making these estimates, our philosophy was to employ the most conservative assumptions possible (those that estimate the smallest number of species), even if those assumptions did not seem the most probable. Our intention was to establish a lower boundary for the number of fungal species that can be revised upward as more information becomes available. Establishing a lower boundary for fungal diversity is important as current estimates vary widely, hindering the ability to include fungi in discussions of ecology, biodiversity, and conservation.

Finally, we discuss the biases and limitations of these estimates, and the ways in which increasing our knowledge of plant and fungal diversity would change the estimates.

Materials and methods

Sources of the data

We used the data provided in the preceding chapters plus information on arthropod-associated fungi (Mueller et al. 2006; Hyde et al. 2006; Feuerer 2006; Shearer et al. 2006; Gams 2006; Weir and Hammond 1997; Weir et al. 2002; Weir and Blackwell 2004) as the starting point for our calculations. The authors of these papers were asked to develop a rigorous estimate of global diversity for their fungal group based on a critical assessment of available data and informed predictions of missing data and levels of endemism. To make our estimates we combined the data from these papers with information on plant diversity for major regions of the globe (http://www.plant-talk.org/Pages/Pfacts5.html, http://www.plant-talk.org/Pages/Pfacts9.html; Mueller et al. 2006). After global species estimates were calculated for each of the six fungal groups (see below), we totaled the estimates to derive an estimate for minimum total fungal species diversity.

Predicting species diversity—macrofungi, lichens, aquatic fungi

As macrofungi, lichens, and aquatic fungi are better known than are other groups of fungi, particularly in terms of geographic distribution, we were able to estimate their minimum species diversity based on geographic data. The first step was to divide the globe into several regions and determine the known fungal species richness of each region. We needed to balance two competing concerns while assembling these data: (1) dividing the globe into many small units to give a fine scale depiction of fungal diversity but with many regions largely unknown, versus (2) employing relatively large and coarse geographic units with some data available for all regions. Knowledge of fungal diversity in many regions is rudimentary, and summary data is very scarce, particularly for the tropics. We decided that dividing the world into fewer,

larger areas better fit the available information. Thus, we divided the world into the following regions: Africa, Central and South America, Europe, North America, temperate Asia, tropical Asia, and Australasia. This enabled us to most accurately depict fungal diversity and distributions based on the extent of our knowledge.

We divided the estimated number of fungi in each of these three groups, in each region, by the corresponding number of plants in that region to get the regional ratio of fungi to plants (the "*F*:*P* ratio"). We then used these ratios to estimate minimum global species diversity. The estimates were made by dividing the regions listed above into a temperate set (Australasia, Europe, North America, and Temperate Asia) and a tropical set (Africa, Central and South America, and Tropical Asia). Unfortunately, the resolution of the data did not permit us to separate the temperate regions of South America and Africa from the rest of the data.

To make the estimate, we used the region within each set with the highest *F*:*P* ratio. We assumed that those two regions (one temperate and one tropical) had been completely inventoried. Obviously, this assumption is not true, but by assuming a complete inventory we ensured that our estimate was biased towards predicting a low number of extant fungal species. We then multiplied the number of plant species in each of the remaining temperate regions by the highest *F*:*P* ratio from the temperate regions and multiplied the number of plants in each of the remaining tropical regions by the highest *F*:*P* ratio from the tropical regions. This gave us the predicted fungal species diversity for each region.

We then calculated the predicted global species diversity for each fungal group from the regional predictions. Because many fungal species are known to be present in more than one region, we could not simply add up the regional predictions to get a global prediction. Therefore, we used the compiled list of names for each fungal group to estimate the amount of overlap between regions for that group. We divided the total number of species known from each fungal group worldwide by the sum of the species known from that group from each region. This gave us a value we call the "overlap factor." We then multiplied the sum of the regional predictions for each group by its overlap factor to make a global species diversity prediction for each fungal group.

This process can be summarized by the following equation:

$$S_{\text{total}} = \left[\sum\nolimits_{\text{temperate}} (P_{\text{r}})\left(F{:}P_{\text{temp}}\right) + \sum\nolimits_{\text{tropical}} (P_{\text{r}})\left(F{:}P_{\text{trop}}\right)\right](V) \qquad (1)$$

where S_{total} is the total estimated number of fungal species worldwide in a particular group, $\Sigma_{\text{temperate}}$ is the summation over the temperate regions, Σ_{tropical} is the summation over the tropical regions, P_{r} is the plant species diversity of a particular region, $F{:}P_{\text{temp}}$ is the maximum *F*:*P* ratio found in temperate regions, $F{:}P_{\text{trop}}$ is the maximum *F*:*P* ratio found in tropical regions and V is the overlap factor.

Predicting species diversity—plant and arthropod-associated microfungi and soil fungi

There is little geographic summary data available for plant and arthropod-associated microfungi (Hyde et al. 2006; Weir and Hammond 1997; Weir et al. 2002; Weir and Blackwell 2004), so we based our estimates on putative ratios of fungi to host

species. Geographic summary data are also lacking for soil fungi, but these fungi are reported to be largely cosmopolitan (Gams 2006).

Results

A total of 78,925 species names were compiled for the six fungal groups (Weir and Hammond 1997; Weir et al. 2002; Weir and Blackwell 2004; Mueller et al. 2006; Hyde et al. 2006; Feuerer 2006; Shearer et al. 2006; Gams 2006). As summarized in Table 1, there is considerable variation in species diversity and overlap factors among these six groups. Approximately half of the recorded fungal names are of lichens and macrofungi with the other half corresponding to microfungi.

Macrofungi

For macrofungi, the regions with the highest *F*:*P* ratios are Europe in the temperate set and Central and South America in the tropical set (Table 2). The overlap factor for macrofungi is 0.75, indicating a moderate number of species are distributed in more than one region. Our estimate for minimum global macrofungal species diversity is 49,500, which is close to the low end of the estimate diversity (53,000–110,000) for this group presented in Mueller et al. (2006).

Lichens

For lichens, the regions with the highest *F*:*P* ratios are Australasia in the temperate set and Tropical Asia in the tropical set (Table 3). The overlap factor for lichens is 0.36 indicating that many species are distributed in more than one region. The minimum estimate for global lichen species is 20,000, which is nearly identical to the estimate of 18,882 species given in Feuerer (2006) and 18,000 species from Sipman and Aptroot (2001).

Lichenicolous fungi

Lichenicolous fungi are those that grow on lichens, but are not part of the lichen itself. Lawry and Diederich (2003) list 1,559 known species of lichenicolous fungi. Hawksworth (2001) estimates that there are between 3,000 and 4,000 total species. We take 3,000 species as a conservative estimate.

Aquatic fungi

For aquatic microfungi, the regions with the highest *F*:*P* ratios are Europe in the temperate set and Tropical Asia in the tropical set (Table 4). The overlap factor for aquatic microfungi is 0.92 indicating that few species are distributed in more than one region. The minimum estimate for global aquatic microfungal species is 8,400. Shearer et al. (2006) report that there are 3,400 recorded species of aquatic fungi, but state that many species remain undescribed.

Table 1 Total described species of fungi and vascular plants by region. Fungal data are from Weir and Hammond (1997), Weir et al. (2002), Mueller et al. (2006), Hyde et al. (2006), Feuerer (2006), Shearer et al. (2006), Gams (2006). Plant data are from *Plant Talk on line, The Diversity of the Plant Kingdom* (http://www.plant-talk.org/Pages/Pfacts5.html, http://www.plant-talk.org/Pages/Pfacts9.html)

Ecological group	Total species described	Australasia	Europe	North America	Temperate Asia	Africa	Central and South America	Tropical Asia	Overlap factor (*V*)
Vascular plants	275,000	16,000	12,500	20,000	45,000	50,000	85,000	46,000	
Lichenized fungi	13,000	5,000	3,640	3,250	2,800	7,200	7,575	7,000	0.36
Macrofungi	21,679	3,880	6,827	10,000	2,675	2,250	6,595	400	0.75
Microfungi									
Aquatic	3,196	242	713	765	226	382	272	869	0.92
Insect-associated	2,750	?	?	?	?	?	?	?	?
Soil-inhabiting	3,300	?	?	?	?	?	?	?	?
Terrestrial plant-associated	35,000	?	?	?	?	?	?	?	?

Table 2 Estimating macrofungal species richness

Region	Vascular plants	Macrofungi	*F*:*P* Ratio	Estimate
Temperate regions				
Australasia	16,000	3,880	0.24	8,800
Europe	12,500	6,827	0.55	6,875
N. America	20,000	10,000	0.50	11,000
Temperate Asia	45,000	2,675	0.06	24,750
Tropical regions				
Africa	50,000	2,250	0.05	4,000
Central and S. America	85,000	6,595	0.08	6,800
Tropical Asia	46,000	400	0.01	3,680
Total *(0.75)				49,429

Table 3 Estimating lichen species richness

Region	Vascular plants	Lichens	*F*:*P* Ratio	Estimate
Temperate regions				
Australasia	16,000	5,000	0.31	5,000
Europe	12,500	3,640	0.29	3,875
N. America	20,000	3,250	0.16	6,200
Temperate Asia	45,000	2,800	0.06	13,950
Tropical regions				
Africa	50,000	7,200	0.14	7,500
Central and S. America	85,000	7,575	0.09	12,750
Tropical Asia	46,000	7,000	0.15	6,900
Total *(0.36)				20,259

Table 4 Estimating aquatic microfungal species richness

Region	Vascular plants	Aquatic microfungi	*F*:*P* Ratio	Estimate
Temperate regions				
Australasia	16,000	329	0.02	1,280
Europe	12,500	1,060	0.08	1,060
N. America	20,000	1,045	0.05	1,600
Temperate Asia	45,000	470	0.01	3,600
Tropical regions				
Africa	50,000	502	0.01	1,000
Central and S. America	85,000	272	0.006	1,700
Tropical Asia	46,000	790	0.02	790
Total *(0.92)				10,147

Soil-inhabiting fungi

Gams (2006**)** estimates that approximately 3,300 soil-inhabiting fungal species have been discovered and that this represents over 30% of the total species. Conservatively assuming that 3,300 species represents 40% of the total soil-inhabiting fungi, there are approximately 8,250 soil-inhabiting species.

Terrestrial plant-associated fungi

As discussed by Hyde et al. (2006) there is relatively little comprehensive information on host or geographic distribution of microfungi associated with terrestrial plants. However, the current evidence clearly indicates that many fungal species are associated with individual plant species, and many of these species are currently known from only a single plant host. Without more data, it is not possible to obtain a rigorous estimate of the ratio of fungi to plants, worldwide. However, given the high richness of fungi on individual plant species and the apparent high level of host specificity (Hyde et al. 2006), in our opinion, a conservative estimate would be that there are two microfungal species for every terrestrial plant species. A ratio of two microfungi per plant is well below that previously published (e.g., Hawksworth 1998). This would lead to a minimum estimate of 600,000 plant-associated microfungi, assuming that there are 300,000 terrestrial plants worldwide.

Arthropod-associated fungi

Currently, there are approximately 2,000 known Laboulbeniales species (Weir and Hammond 1997; Weir et al. 2002; Weir and Blackwell 2004) and approximately 250 known trichomycete species (Lichtwardt et al. 2001). Suh et al. (2005) found 650 yeasts living in beetle guts. Benjamin et al. (2004) and Barron (2004) list less than 1,000 species for other groups of arthropod- and invertebrate-associated fungi. Based on host specificity data, Weir and Hammond (1997) estimated that there are between 20,000 and 50,000 Laboulbeniales species remaining to be found. We use 20,000 species as a conservative estimate for all insect-associated fungi.

Microsporidians

Microsporidians are extremely reduced intra-cellular parasites, primarily of animals (Keeling and Fast 2002). Although they were long thought to be an extremely basal group of eukaryotes, recent phylogenetic analysis has demonstrated that they are highly reduced fungi instead (Gill and Fast 2006). There are 1,200 known species (Keeling and Fast 2002). We take this number as a conservative estimate of their diversity although it is likely that many more await discovery.

Totals

In total, we estimate that there is a minimum of 712,285 fungal species worldwide, over 82% of which are microfungi associated with terrestrial plants. Approximately 13% of these species have already been described, but only 7% of the plant-associated microfungi have been described.

Discussion

Our minimum estimate of over 712,000 species is lower than most previous estimates of fungal species diversity (summarized in Hawksworth 2001). However, we intentionally used very conservative assumptions at all stages of our analyses, as our goal

was to establish a lower boundary for the number of fungal species. This estimate will be revised upward as more information becomes available. Even so, our analyses suggest that earlier estimates of 500,000 fungal species (May 1991) are unrealistically low. Some groups of fungi, such as endolithic fungi and most that are pathogens of organisms other than plants or arthropods, are not included in this estimate. While these groups of fungi are not currently known to be speciose, their exclusion makes our estimate even more conservative.

Arthropod- and terrestrial plant-associated microfungi are clearly the two groups whose species diversity is hardest to assess at this time. For example, a single recent study added over 20% to the number or known yeast species by surveying yeasts found in beetles (Suh et al 2005; Boekhout 2005). Arthropod- and terrestrial plant-associated fungi are also the two groups that could most influence fungal diversity estimates. Both groups are clearly very diverse, but comprehensive data on their geographic distributions and host/substrata specificity have not yet been compiled. Distribution data, used in conjunction with estimates based on ratios of fungal species to host species, for these fungi are necessary to more accurately estimate the true diversity of fungi.

Impact of additional plant species diversity information

It is important to understand how additional information about plant and fungal species diversity and distributions will change these estimates to assess the accuracy and improve the utility of calculating ratio data for generating diversity predictions.

Obviously, the estimate for terrestrial plant-associated microfungi is based on fungus to host ratios, so changes in that ratio will result in a proportional change in the estimated number of fungal species. It might also be expected that the discovery of many new plant species would make dramatic changes to the fungal diversity estimates based on the ratio estimates derived from Eq. 1. However, this is not necessarily the case. As an extreme example, if the number of plant species were to double in every region, our estimates of fungal species diversity from Eq. 1 would not change. The ratios of plants to fungi, *F*:*P*, would be half of what is reported in the Tables 2–4, but when multiplied against the higher number of plants it would result in the same estimate of fungal diversity.

Minimum fungal diversity estimates from Eq. 1 are sensitive to differences in plant species diversity among regions. If future research results in greatly increasing the plant species diversity of one region, but not others, this could either increase or decrease the global fungal diversity estimates depending on what region was involved. As an extreme example, suppose the number of plant species known from Europe were to double, but the remaining regions were to remain the same. This would change the macrofungus to plant ratio in Europe from 0.55 to 0.27 (Table 2), and North America would then be the region with the highest *F*:*P* ratio at 0.50. Looking at the temperate region, the estimates of macrofungal species diversity would drop to 8,000 for Australasia, to 10,000 for North America, and 22,500 for Temperate Asia, whereas the estimate for Europe would increase to 12,500. These contrasting changes occur because Europe currently has the highest *F*:*P* ratio for macrofungi. If the number of plant species in North America was doubled, but all other regions remained the same, then the estimated number of macrofungi for North America would double to 22,000, but the estimates for the other regions would remain the same. While such drastic changes in our understanding of plant

species diversity are unlikely to occur, smaller changes are likely. The impact of these changes on the estimates depends on which regions see a relative increase compared to other regions, and whether the affected region has the highest *F*:*P* ratio for the group of fungi involved.

Impact of additional information on fungal species diversity

Improved information on fungal species diversity can be used for two goals in relation to these estimates: improving the estimates and verifying the estimates. Unfortunately, information that is ideal for improving the estimates is less useful for verifying them. For estimates based on Eq. 1, finding new species of fungi in the best known regions will increase the *F*:*P* ratios, which in turn will cause an increase in the estimates for all other regions and the global estimate. This will not, however, help determine if using plant/fungus ratios is an effective way to estimate fungal species diversity.

To determine the accuracy of ratio estimates, more information is needed about species diversity in poorly studied areas. Undersampled areas need to be inventoried to determine if the *F*:*P* ratio is constant regardless of habitat. In practice, such a survey will not be possible for anything but small areas (1 ha or less) because of the difficulties in sampling all fungi. However, even determining the amount of variation in the *F*:*P* ratio on small plots would help to determine if ratio estimates are a reasonable way to determine fungal species diversity. A recent meta-analysis of fungal diversity studies on small plots (Schmit et al. 2005) demonstrated that tree species and macrofungal species diversity are correlated. While this result supports the use of ratio estimates for fungal diversity, more work on a greater variety of fungi and habitats is needed.

Factors not accounted for by ratio estimates

While ratio estimates are a promising method for estimating fungal species diversity, they have many limitations. It is possible that the species diversity of some groups of fungi may follow that of plants whereas others do not. Insect-associated fungi are likely to be an extremely diverse group, but the species diversity of these fungi is likely to be directly tied to that of insects rather than plants. Given the high degree of uncertainty surrounding insect species diversity (Ødegaard 2000), estimates of insect-associated fungal diversity are likely to be uncertain for the foreseeable future. However, plant diversity can influence the diversity of insects and their associated fungi, so in the future plant diversity may aid in estimating the diversity of insect-associated fungi (Hawksworth, 1998).

Secondly, some groups of fungi may not be suited to ratio estimates. For example, lichen-forming fungi often comprise the dominant vegetation in alpine and polar environments, and as such they are not closely associated with vascular plant diversity. However, in other environments they are dominant epiphytes. It may be that lichenized fungal species diversity is more closely related to the structure of the habitat than to the species diversity of vascular plants per se.

Thirdly, it may be that ratios can be used to estimate fungal species diversity within major habitat types (e.g., temperate deciduous forest, boreal coniferous forest, etc.) but are less reliable when used across habitat types. The separation of the tropical regions from the temperate regions in Tables 2–4 is an initial step in assessing the potential impact such differences would have on our estimates of fungal species diversity. The small amount of data that are available indicate that tropical zones have a higher species diversity than temperate zones (Hawksworth 2001), which is necessary for *F*:*P* ratios to be constant across major habitats.

Finally, mycologists are becoming increasingly aware of the phenomenon of ''hidden'' or ''cryptic species''—species that look identical or nearly identical morphologically but are in fact distinct species (Hawksworth 2001; Hawksworth and Mueller 2005). Cryptic species have been found in a wide variety of fungal groups (Hawksworth 2004). Currently it is difficult to estimate how many cryptic species are lurking within accepted species; however, it has been estimated that adoption of a biological species concept could result in a five-fold increase in known species in some fungal groups (Hawksworth and Rossman 1997).

Cryptic species are likely the greatest challenge in accurately estimating fungal diversity. The high number of cryptic species implies that mycologists have actually collected many more species than have been recognized. As all estimates of fungal diversity are based on known species, our inability to fully account for cryptic species not only results in an underestimation of species diversity within regions and but likely leads to an overestimation of the overlap between regions. The overestimation of the overlap is due to the fact that two distinct species found in two different regions may be combined under a single name, making the regions appear more similar than they actually are. Both types of errors lead to an underestimate of total fungal species diversity. To correct for this bias, we would need to determine how many currently recognized species harbor unknown cryptic species. This would require information on a wide variety of fungal species, including instances where mycologist cannot find cryptic species.

Research needs

Additional fungal surveys, especially in undersampled tropical regions, and rigorous monographic treatments to resolve species circumscriptions and distributions are crucial to improve our knowledge of species diversity. However, other research needs also exist.

While nearly 80,000 fungal species have been described (Kirk et al. 2001), information about them, their geographic distribution, and plant or insect hosts is widely scattered. Compiling the already available information into publicly available databases would enable researchers to make significant progress in understanding fungal diversity and biogeography.

While ratio and other types of estimates may be useful, they are not based on well-proven ecological principles. Rather they are based on the reasonable, but as yet untested, notion that there is some causal link between the species diversity of various groups at various geographic and taxonomic scales. Studies at small scales are needed to elucidate if this is so, and to determine if there are consistent ratios between plants, arthropods, and fungi over various geographic scales.

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