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ORIGINAL PAPER

Global diversity and distribution of macrofungi

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Abstract Data on macrofungal diversity and distribution patterns were compiled for major geographical regions of the world. Macrofungi are defined here to include ascomycetes and basidiomycetes with large, easily observed spore-bearing structures that form above or below ground. Each coauthor either provided data on a particular taxonomic group of macrofungi or information on the macrofungi of a specific

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geographic area. We then employed a meta-analysis to investigate species overlaps between areas, levels of endemism, centers of diversity, and estimated percent of species known for each taxonomic group for each geographic area and for the combined macrofungal data set. Thus, the study provides both a meta-analysis of current data and a gap assessment to help identify research needs. In all, 21,679 names of macrofungi were compiled. The percentage of unique names for each region ranged from 37% for temperate Asia to 72% for Australasia. Approximately 35,000 macrofungal species were estimated to be ''unknown'' by the contributing authors. This would give an estimated total of 56,679 macrofungi. Our compiled species list does not include data from most of S.E. Europe, Africa, western Asia, or tropical eastern Asia. Even so, combining our list of names with the estimates from contributing authors is in line with our calculated estimate of between 53,000 and 110,000 macrofungal species derived using plant/macrofungal species ratio data. The estimates developed in this study are consistent with a hypothesis of high overall fungal species diversity.

Keywords Ascomycetes · Basidiomycetes · Biodiversity · Biogeography · Endemism · Species lists

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Introduction

Although macrofungi have perhaps the longest history of diversity studies of any group of fungi, they are nevertheless understudied over most of the world. More data are available from North America and Europe than from any other region, but knowledge of macrofungal diversity is incomplete even for these regions. Taxonomic obstacles, a paucity of trained mycologists, and the low number of published, rigorous, long-term studies prevent us from conclusively answering even basic questions about the number of macrofungal species at a specific location, or whether macrofungal diversity is greater in one type of forest than in another.

To address this situation, we compiled information on current knowledge of macrofungal diversity by compiling species lists from the literature and unpublished data from contributing authors to generate an estimate of ''actual'' global macrofungal diversity based on ratios of plant–fungus diversity and levels of endemism. We also undertook a gap assessment of the compiled data to help identify research needs. We used a simple definition for macrofungi when compiling data for this study. Macrofungi are distinguished by having spore-bearing structures visible to the naked eye (mushrooms, brackets, puffballs, false-truffles, cup fungi, etc.). Most macrofungi are Ascomycota or Basidiomycota, but a few are Zygomycota. Most terrestrial macrofungi are saprobes or mycorrhizal symbionts, but some are pathogens of plants or fungi. Fungi fruiting on woody substrata are usually either saprobes or plant pathogens.

Materials and methods

Published and unpublished species lists were compiled for major regions of the world to generate a list of macrofungal names (Table 1). We emphasize that these are lists of names, not taxa, as many of the employed lists are not supported by voucher collections so we could not check the accuracy of the included names. Efforts were made to correct for nomenclatural synonyms and to eliminate superfluous names. Data on some specific macrofungal groups' diversity, degrees of endemism, and estimates of undiscovered taxa were also compiled (Table 2).

The edited lists of names for each region were compared to determine the percent of names that were unique to each region (a proxy for estimates of endemism). Diversity estimates for each region were then generated using different plant species to macrofungal species ratios. Global estimates were generated based on these regional estimates assuming different levels of endemism.

Each contributing author was asked to make an informed estimate of the ''true'' diversity and levels of endemism for their region or macrofungal group. These informed estimates were used to assess the potential accuracy of the generated predictions.

Results

In all, 21,679 names of macrofungi were compiled; half of which were from North America and Western Europe. Estimates of ''unknown'' macrofungal species from contributing authors totaled approximately 35,000 species.

Table 1 Sources of data for each region

North America
Field museum fungal collections database
Checklist from North American Mycological Association national forays, Field Museum
MICH fungal herbarium database, R. Fogel
Taxa from NA literature, S. Redhead (database)
Collybia of NE USA, R. E. Halling 1997(website)
Fungi of Rocky Mountain Alpine, C. Cripps and E. Horak 2002 (website)
Weber and Smith 1985
Kimbrough 2000
Metzler and Metzler 1992
Bessette et al. 1997
Lincoff 1995
Phillips 1991
Arora 1986
Hesler and Smith 1979
Kibby and Fatto 1990
Redhead 1989
Mexico, Central America and Caribbean
New records from Mexico, J. Cifuentes (database)
Neotropical Macrofungi in New York Bot. Garden Herbarium, R. E. Halling (database)
Macrofungi of the Greater Antilles, D. J. Lodge and T. Baroni (database)
Pegler 1983
Herrera and Guzmán 1972
Bandala-Muñoz et al. 1988

Tropical South America
Tropical Ascomycetes, T. Iturriaga (database)
Xylariaceae in the Neotropics, T. Iturriaga and D. Minter (database)
Taxa described by Rolf Singer, Q.X. Wu and G. Mueller, (Field Museum database)
Dennis 1970
Pegler 1997
Temperate South America
Checklist of South Temperate Macrofungi, M. Rajchenberg (database)
Singer 1969
Horak 1979
Garrido 1988
Mujica and Vergara 1980
Valenzuela 1993
Greslebin 2002
Greslebin and Rajchenberg 2003

Antarctica
Greene et al. 1967
Temperate Asia (China and Japan)
Checklist of Temperate Asia Macrofungi, Database compiled by Q. X. Wu
Africa
Agaricales Fungi in AFRICA Herbarium, Belgium National Herbarium (website)
Flore Iconographique des Champignons du Congo, Fasc. 1 –17. 1935–1970
Pegler 1977
Buyck 1996
Europe
The GB checklist of fungi-genus/species list, 4© BMS 2000. Pages by Jerry Cooper
Taxa in the Mycological Herbarium, Copyright for all lists: © The Herbarium, The Natural History Museums and Botanical Garden, University of Oslo
Fungi of Poland (and Czech Republic pro part), (website http://www.grzyby.pl/)
Moser 1983
Breitenbach and Kränzlin 1986, 1991, 1995, 2000
Nauta and Vellinga 1995
Dimou et al. 2002

Table 1 continued

Tropical Asia
Select Agarics and Boletes from Malaysia, R. Watling (summary data)
Hawaii
Agaricales of The Hawaiian Islands, D. Desjardin and D. Hemmes (database)
Hemmes and Desjardin 2002
Australasia
Australia
May and Wood 1997.
May et al. 2002
New Zealand
Segedin and Pennycook 2001
Petersen 1988
Cunningham 1944
New Caledonia
Horak and Mouchacca 1998
New Guinea
Shaw 1984
Desjardin 1995
Desjardin and Horak 1997a, b
Additional data
Schmit et al. 2005

Table 2 Sources of data for select macrofungal groups

Sequestrate fungi
Global diversity and distribution of hypogeous fungi, J. Trappe (summary data)
Polypores
Global diversity and distribution of polypores, L. Ryvarden (summary data)
Corticioid fungi
Global diversity and distribution of corticioid fungi, K.-H. Larsson & K. Hjortstam (summary data)
Xylariaceae
Tropical species of Xylariaceae, T. Itturiaga and D. Minter (summary data)

The percentage of unique names in our compiled data set for each region ranged from 37% for temperate Asia to 72% for Australasia (Table 3). However, levels of endemism vary greatly among the different taxonomic and ecological groups of macrofungi. For example, among wood inhabiting non-fleshy fungi, polyporoid fungi display low levels of endemism, with corticioid fungi showing only slightly higher levels of endemism than polyporoid fungi (Tables 4, 5). Conversely, sequestrate fungi (hypogeous truffles and false-truffles) and the Xylariaceae (Ascomycota) show relatively high levels of endemism (Tables 6, 7). Thus, generalities regarding endemism for macrofungi are difficult to formulate.

As a starting point for generating a global estimate of macrofungal diversity, we assumed (for this paper only) that the compiled list of names of macrofungi for North America and Europe gives us a true and nearly complete indication of species diversity for these two regions. Comparing these figures, 10,000 and 6,827 for North America and Europe, respectively, to documented plant species diversity data, 20,000 and 12,500 species for North America and Europe, respectively (http://www.plant-talk.org/Pages/Pfacts2.html) we arrive at a flowering plant species to

Table 3 Number of taxon names compiled for each region during this study followed by the percent of unique names for that region

Region	# of names recorded	Unique names[a](%)
North America	10,000	65
Tropical America (Central and South America)	5,680	70
Temperate South America	915	64
Western Europe	6,827	60
Africa	2,250	70
Temperate Asia	2,675	37
Tropical Asia	400[b]	43
Australasia (Australia, New Caledonia, New Guinea, and New Zealand)	3,880	72
Hawaii	683	40
Total names compiled	21,679	

[a] excluding polypores, corticioids, and hypogeous fungi

[b] Only from a small data set on select agarics and boletes from Malaysia submitted by R. Watling

Table 4 Corticiaceae data from K.-H. Larsson and K. Hjortstam

	Region	Known species	% edemic to region	Estimated unknown
Polar				
	Arctic	0	0	50/100%
	Antarctic	0	0	50/100%
Western hemisphere				
	Boreal	344	9	280/45%
	N. temperate	605	17	400/40%
	Tropics	598	31	900/60%
	S. temperate	83	28	420/83%
Eastern hemisphere				
	Boreal	478	6	150/24%
	European temperate	611	11	240/28%
	Asian temperate	507	23	500/50%
	Northern Africa	177	4	220/56%
	Tropical Africa	483	36	1000/68%
	Madagascar	16	6	580/97%
	Temperate Africa	65	17	440/87%
	Mid East	18	6	380/95%
	Tropical Asia[a]	259	29	1250/83%
	Australasia	165	9	840/83%
	Pacific Islands	234	32	470/67%
Total		1,853		

[a] Tropical Asia includes Indonesia, Philippines, Malaysia and New Guinea

macrofungus species ratio of 2:1. Extrapolating this ratio of two species of flowering plants to each macrofungal species using the reported plant species diversity data for each region (see Mueller and Schmit this issue) gives us a very high diversity estimate for macrofungi; 85,000–110,000 depending on the employed degree of endemism (Table 9). A more realistic estimate for macrofungal diversity, 53,000–65,000, was obtained when using two different plant/macrofungus ratios—2:1 for temperate regions and 5:1 for tropical regions (Table 9). Several different ratios were tried for

Table 5 Species diversity and distribution of Polypores; Data from L. Ryvarden

Region	# of Species	
North America	420	70% overlap between Europe and North America
Tropical America	480	15% overlap between Europe and Africa
Europe	377	80% overlap between East Asia and North America
Tropical Africa (excluding *Ganoderma* species)	360	55% overlap between tropical Africa and the Neotropics
North East Asia	472	70% overlap between tropical Africa and Asia
New Zealand	169	85% overlap between New Zealand and Australia
Australia	290	
Total	1,200	

Table 6 Diversity and distribution data on sequestrate fungi (hypogeous truffles and false truffles). Data compiled by J. Trappe

	Region	Known species	% endemic to region	Estimated unknown species
Polar				
	Arctic	2	0	10
	Antarctic	0	0	0
Western hemisphere				
	Boreal	10	0	40
	N. temperate	400	50	600
	Tropics	30	25	200
	S. temperate	30	95	300
Eastern hemisphere				
	Boreal	10	0	40
	European temperate	250	40	50
	Asian temperate	50	40	750
	Northern Africa	30	20	200
	Southern Africa	10	90	100
	Madagascar	5	90	50
	Temperate Africa	5	75	300
	Mid East	20	20	100
	Tropical Asia[a]	20	80	1,000
	Australasia	250	95	1,500
Pacific islands		5	10	50
Total estimated species (known + unknown) =4,500–5,500				

[a] Tropical Asia includes Indonesia, Philippines, Malaysia and New Guinea

tropical regions (data not shown). The 5:1 ratio gave results in line with *a priori* estimates provided by coauthors for tropical America and Hawaii. Available information on African and tropical Asian macrofungi is too scant to assess the potential accuracy of these estimates for those regions.

Table 7 Known species diversity and levels of endemism for tropical species of Xylariaceae (Ascomycota). Data compiled by T. Iturriaga and D. Minter

	Venezuela	Caribbean	Canary islands	China, tropical	México
Venezuela	144[a]				
Caribbean	89[b]	275			
Canary islands	7	9	21		
China, tropical	29	45	9	123	
México	80	122	6	33	272

[a] Number of species in that country or region

Summary and conclusion

Using lists of names to estimate species numbers is not ideal. We know that we have inadvertently included synonyms and some superfluous names. However, the data sets for each region are often woefully incomplete and most taxonomic groups have not been recently monographed, so numerous cryptic species will likely be uncovered. Therefore, we are confident that our numbers represent very conservative estimates for macrofungal diversity in each region.

A total of 21,679 names of macrofungi were compiled. An additional approximately 35,000 macrofungal species were estimated to be ''unknown'' by the contributing authors. This would give an estimated total of 56,679 macrofungi. Our compiled species list includes little to no data from most of S.E. Europe, Africa, western Asia, or tropical eastern Asia. Even so, combining our list of names with the *a priori* estimated numbers of taxa awaiting discovery provided by collaborating authors is in line with our calculated estimate of between 53,000 and 110,000 macrofungal species generated using plant/macrofungal species ratio data (Table 9). Our calculations return an estimate close to the projected diversity for macrofungi of 140,000 species postulated by Hawksworth (2001). Assuming that the 21,679 species names that we compiled during this study is an accurate indicator of the number of ''known'' macrofungi, 16–41% of macrofungi have been described to date.

Using a higher ratio of plants to macrofungi in tropical regions than for temperate areas gave a more realistic estimate of macrofungal diversity for countries for which enough data exist to make meaningful *a priori* estimates, e.g., using the 5:1 plant species to macrofungus species ratio for Costa Rica, home to roughly 10,000 plant species yields an estimate of 2,000 macrofungal species which is in line with the estimate of 1,500–2,500 macrofungal species being used by the Costa Rican National Fungal Inventory (Halling and Mueller 1996; Mueller and Mata 2000; Mueller et al. 2006). Comparing data in Tables 3 and 9, we predict that roughly 1/2 of the macrofungal diversity for tropical South America has been recorded to date (14,000 species estimated with 6,595 names compiled). This is consistent with our *a priori* predictions (author estimates). Using the 5:1 ratio also generates a macrofungal diversity estimate closely in-line with estimates generated during Hemmes and Desjardin's multiyear macrofungal inventory of Hawaii (Hemmes and Desjardin 2002; Tables 8, 9). Likewise, the 2:1 ratio for temperate regions yields a prediction of 8,000 species for Australasia, which is close to the 9,000 macrofungal species estimate for the region (Tables 4, 6 for Corticiaceae and sequestrate fungi, respectively plus estimate for euagarics by T. W. May, personal communication). Using the 2:1 ratio gives us a prediction of 3,000 macrofungi for temperate South America, which

Table 8 Diversity of Hawaiian macrofungi. Data generated by D. Desjardin and D. Hemmes

Taxon	Known species	% endemic to region	Estimated unknown
Macrofungi (total)	643[a]	15.4%	450
Macrofungi (native)	125	80%[b]	50
Plants (total)	5,600[c]		
Angiosperms (native and naturalized)[d]	1,817[d]	46%[d]	
Angiosperms (native)	956[d]	89%[d]	44[d]

[a] Agaricales, gasteromycetes, jelly fungi, and Aphyllophorales growing with both native and introduced plant species; many of them on debris or wood of introduced conifers)

[b] 99 endemic species out of 125 native macrofungi species

[c] Data from Cuddihy and Stone 1990

[d] Data from Wagner et al. 1990

Table 9 Estimates for global species diversity of macrofungi based on two assumptions of the ratio between macrofungal and flowering plant species diversity: (a) 2:1; two plant species to each species of macrofungus in each region, and (b) 2:1 and 5:1; two plant species per macrofungus species in temperate zones and five plant species per macrofungus species for tropical regions

Region	Flowering plant to macrofungal species ratio employed	
	2:1	2:1 for temperate zone 5:1 for tropical zone
North America	10,000	10,000
Central America	15,000	6,000
Tropical South America	35,000	14,000
Temperate South America	3,000	3,000
Western Europe	6,250	6,250
Africa	25,000	10,000
Temperate Asia	22,500	22,500
Tropical Asia	25,000	10,000
Australasia	8,000	8,000
Hawaii		
Total macrofungi/total flora	2,800	1,120
Native macrofungi/native flora	478	191
Estimated totals for world[a]	85,000–110,000	53,000–65,000

[a] Estimated totals of global diversity are given as ranges as the estimates depend on the level of endemism for each region. Estimates of endemism per region based on data presented in Tables 3–6, and 8

would imply that only approximately 1/3 of the macromycota of the region has been documented (915 names; Table 3). However, much of temperate South America is grasslands or semi-deserts, so a more accurate predictor would be based on the number of plants recorded from the Valdivian and Tierra Del Fuegan Forest regions since this is where most macrofungi occur and are the areas that have been sampled for macrofungi. Using these numbers, nearly half of the regions estimated macrofungal diversity has been recorded (915 macrofungi for 4,000 plants). While these estimates can only be used as rough indicators of potential regional diversity, the data document that macrofungal diversity is high, and that most regions of the world are severely undersampled, irrespective of employed ratio.

Each region's list of names included a high proportion of unique names (40–72%). If this estimate of endemism is true, endemism levels in macrofungi approach the levels seen at continental scales for vascular plants. A recent meta-analysis of point diversity studies of macrofungi generated data consistent with plants and macrofungi having similar levels of continental endemism as the authors uncovered no significant difference in distribution ranges between macrofungi and trees in the included studies (Schmit et al. 2005).

The estimates developed in this study are consistent with a hypothesis of high overall fungal species diversity. Macrofungi putatively comprise 10% of total fungal diversity (Rossman 1994). If this estimate is correct, extrapolating our estimate of 53,000– 110,000 of macrofungi to Fungi would give an estimate of 530,000–1.1 million species of fungi. Unfortunately, these estimates cannot be further tested without data from in-depth inventories of macrofungi and other fungi from a number of areas in the world, especially tropical regions of South and Central America, Africa and tropical Asia. Both large scale (regional level) and point-based (site level) data are needed to assess plant/macrofungal species ratios and to obtain data to document levels of macrofungal endemism.

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