

A Survey of Patterns of Diversity in Non-Lichenized Fungi

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Abstract

This paper summarizes the opinions of 26 mycologists who have worked in more than one hemisphere or continent regarding the locations, correlates, and potential causes of centers of fungal endemism and diversity in non-lichenized fungi. These views were initially obtained via a survey and then summarized by the lead author. Most authors working on basidiomycetes thought that fungal diversity was more strongly correlated with host and habitat diversity than with resource abundance, whereas most of those working on ascomycetes and Hyphomycetes indicated that all three factors were very important. Overall diversity was highest in the tropics, at intermediate to high rainfall, and at middle to low elevations. Certain fungal groups, however, such as the Cortinariaceae (Agaricales), and some members of the Heterobasidiomycetes are more diverse at middle to high latitudes and elevations. There was no apparent variation in Gasteromycete diversity with latitude. The Neotropics were ranked as having a greater diversity of fungi than Africa by three of the four authors with experience in both. Although this pattern might be related to historical factors or to a higher diversity of host plants in the Neotropics, collections of fungi from Africa and the Asian tropics have been too limited to make confident comparisons between continents. Except for the Gasteromycetes and certain plant parasites, Europe was always ranked lowest in fungal diversity when it was included in comparisons, even though collecting has been most intense there.

The types of areas most frequently mentioned as having many species that are unknown elsewhere were humid forests on islands, tropical mountaintops, and large tropical river basins. For example, Australia, New Zealand, New Guinea, Sulawesi, the Andes, and parts of Africa and South America, especially the Congo and Amazon river basins were thought to have many unique species. These areas encompass many wet to moist centers of endemism for plants. The concordance suggests that despite differences in the mechanisms of dispersal and sexual incompatibility, there may be similar forces governing the isolation and speciation of plants and fungi growing in humid areas. Some plant parasitic Heterobasidiomycetes that are host-restricted occur in all regions and habitats, including dry ones. Species with limited ranges also appear to be common in the Agaricales regardless of the region. Unfortunately, there is currently too little knowledge of fungal mating systems and dispersal barriers with regard to their roles in fungal evolution and distribution. The various gaps, hypotheses, and global patterns of fungal diversity identified in this paper are worthy of pursuit through experiments and comparable surveys.

Keywords: fungi, diversity, endemism, dispersal, reproductive isolation, speciation

1 Introduction

There is a growing consensus that there are at least one million, and perhaps 1.5 million or more species of fungi in the world (HAWKSWORTH 1991, 1993; HAMMOND 1992; ROSSMAN 1994). Mycology has been represented in recent forums on global biodiversity (e.g., HAMMOND 1992), but the types of information commonly available for plants and animals is unfortunately often lacking or fragmentary for fungi. Because relatively few mycotas are thoroughly known, it is difficult to know which species have truly restricted geographic ranges, where centers of high diversity lie, and what factors are related to fungal diversity. Such issues are crucial to the conservation of fungal diversity. In the absence of complete knowledge, the expert opinions of mycologists with broad geographical experience are valuable for suggesting where our conservation efforts might be directed with greatest effect in the short term, and for suggesting hypotheses about fungal diversity and evolution that may be worthy of further pursuit and testing. This paper summarizes the opinions of the 26 authors who have studied fungi in more than one hemisphere regarding the locations, correlates, and potential causes of centers of fungal endemism and diversity.

2 Methods

A survey was sent to 22 mycologists who were known to have worked with various basidiomycetes, ascomycetes, or anamorphic stages (asexual states) of non-lichenized fungi on more than one hemisphere or continent. Nineteen of the authors came from this group, and an additional seven came from colleagues of the 22 who were contacted initially. Some authors combined their responses to the survey for a particular group, while others supplied separate information for two different groups. In all, 29 surveys are summarized below, representing 17 for basidiomycetes, one for macrofungi (mostly large basidiomycetes), seven for ascomycetes, and four for fungi that are primarily asexual or vegetative states of ascomycetes (Hyphomycetes and plant endophytic fungi) (Tab. 1). Two responses were for a given genus, seven for families, seven for orders, six for higher taxonomic groupings, two for Hyphomycetes, and four for ecological or other groups (Gasteromycetes, ant-fungus gardens, plant endophytes, and macromycetes). These views were then summarized by the lead author.

The classification of geographical regions into areas of high, intermediate or low rainfall depends on the degree to which moisture losses from evapotranspiration are balanced or exceeded by inputs from precipitation, so it varies with temperature regimes, latitude, and altitude (HOLDRIDGE 1947). The amount of annual precipitation associated with the Rain Forest and Rain Tundra life zones, as defined by HOLDRIDGE (1947), (high rainfall in this survey) is 500-1000 mm in Alpine elevational belts at Subpolar latitudes, 2000-4000 mm in Boreal Subalpine and Cool Temperate Montane areas, 4000-8000 mm in Lower Montane and Premontane elevational belts at Warm Temperate and Subtropical latitudes, and greater than 8000 mm in lowlands at tropical latitudes. Intermediate rainfall, associated with Wet and Moist Forests and Tundra plant formations, occurs with an annual precipitation of 125-500 mm in Alpine elevational belts at Subpolar latitudes, 250-1000 mm in Subalpine elevational belts at Boreal latitudes, 500-2000 mm in Mon-

tane elevational belts at Cool Temperate latitudes, 1000–4000 mm at Lower Montane and Premontane elevational belts at Warm Temperate and Subtropical latitudes, and 2000–8000 mm in tropical lowlands (HOLDRIDGE 1947).

Tab. 1. A list of authors, the fungal groups for which they supplied responses, and the geographic regions in which they have studied them.

Author	Fungal group	Regions
J. Ammirati	Cortinariaceae (Agaricales)	Pacific NW USA
H.H. Burdsall, Jr.	Aphylophorales (Basidiomycotina)	USA, Caribbean
I. Chapela	Endophytic fungi	Britain, Europe, Japan, Mexico
I. Chapela	Fungi of ant-gardens (Agaricales)	Western hemisphere
C.A. Decock and G.L. Hennebert	Aphylophorales (Basidiomycotina)	Amazon basin, tropical Nepal, S. India, Zimbabwe, Europe
D. Desjardin	Agaricales	Hawaiian islands
D. Desjardin	Marasmioid fungi (Agaricales)	World-wide
R. Halling	Agaricales and Boletales	Western hemisphere
G.L. Hennebert	Hyphomycetes	Amazon basin, tropical Africa, Canaries, E. USA, Canada, Europe
E. Horak	Cortinariaceae (Agaricales)	S. South America, Australia, NZ
E. Horak	Entolomataceae (Agaricales)	N. & S. America, Europe, Australia, NZ, New Guinea
S. Huhndorf	Melanommatales (Ascomycotina)	Fr. Guiana, Venezuela, Puerto Rico, and E. USA
P.M. Kirk	Hyphomycetes	S.E. Asia, E. Africa
T. Laessøe	Xylariaceae (Ascomycotina)	S. America, Caribbean, Africa
D.J. Lodge	Tricholomataceae (Agaricales)	C. and S. America, Caribbean
O.K. Miller	Boletales (Basidiomycotina)	Korea, Japan, Nepal, USA, W. Australia, S. Africa, Namibia
O.K. Miller	Gasteromycetes	USA, Canada, Australia, deserts in Africa and Namibia
D.W. Minter	Rytismatales	World-wide database
G. Mueller	Agaricales of temperate forest	Western hemisphere
F. Oberwinkler	Heterobasidiomycetes and Corticiaceae (Basidiomycotina)	World-wide
D.N. Pegler	Homobasidiomycotina	E. and W. Africa, India, Sri Lanka, Malaysia, S. Brazil, Caribbean (L. Antilles), Australia, Europe
R.H. Petersen	Hymenomycetes (Basidiomycotina)	Neotropics, N. America, Europe, E. Russia, New Zealand
J.D. Rogers	Xylariaceae (Ascomycotina)	Mexico, N. America, Asia, New Zealand, Caribbean
L. Ryvardeen	Polyporaceae (Basidiomycotina)	Zimbabwe, Ethiopia, Norway
G. Samuels	Pyrenomycetes (Ascomycotina)	Neotropics, E. USA, NZ, N. Sulawesi
B. Spooner	Discomycetes	Britain, NZ, New Guinea, Brunei
R. Watling and Evelyn Turnbull	Macromycetes (Basidiomycotina)	W. Africa, Peninsular Malaysia
A.J.S. Whalley	Xylariaceae (Ascomycotina)	Philippines, India, Britain
F.A. Uecker	Phomopsis (Ascomycotina)	Britain, Mediterranean, Malaysia

3 Results

3.1 Latitude

Overall diversity is higher at low latitudes in the Hymenomycetes (Homo- and Heterobasidiomycetes, excluding rusts and smuts), and macrofungi (primarily basidiomycetes), but there are mixed patterns of diversity with latitude at lower taxonomic levels (Tab. 2). For example, diversity is greatest at middle latitudes in the Homobasidiomycetes, increases or decreases with latitude among the Heterobasidiomycetes and related corticiaceous Homobasidiomycetes depending on the family or genus (OBERWINKLER 1993), and follows no pattern among the Gasteromycetes as a whole, though certain families or orders, such as the Phallales, are more diverse in the tropics and subtropics (DRING 1980, MILLER and MILLER 1988). The Gasteromycetes are a polyphyletic, ecological group (MALENÇON 1931, REIJNDERS 1963, SMITH and SINGER 1958, HORAK and MOSER 1965, HEIM 1971, BAS 1975, WATLING 1982, MILLER and WATLING 1987, MILLER and MILLER 1988). Among the Aphyllophorales (Cantharellales, Hericiales, Poriales, Ganodermales, Bondarzewiales, Fistulinales, Lachnocladiales, Stereales, and Thelephorales) there was a consensus that diversity was higher at middle and low latitudes than at high latitudes. Within the Aphyllophorales, there are more species of polypore fungi in tropical Africa than in temperate Europe, despite the comparatively light collecting in Africa (Polyporaceae; RYVARDEN 1993). A similar pattern of higher diversity in the New World tropics may occur in the Agaricales. The diversity of agarics associated with ant fungus-gardens, however, is highest in subtropical South America and decreases as one goes north through Central America into temperate North America. Strong latitudinal gradients in diversity were more apparent among some basidiomycetes families, but the direction of the change differed among groups or hemispheres. For example, within the Agaricales, the Cortinariaceae is more diverse at middle to high latitudes in both the northern and southern hemispheres (HORAK 1979, MOSER and HORAK 1975), while the Tricholomataceae and Agaricaceae appear to be more diverse in the tropics (DENNIS 1970). In the New World, the diversity of Boletales decreases as one approaches the equator, but there is no corresponding increase in diversity at higher latitudes in the southern hemisphere. The New World Boletales are mostly ectomycorrhizal symbionts of trees in the Pinaceae, Fagaceae and Salicaceae, and their diversity follows the distribution of their host plants. The high diversity of Boletales associated with trees in the Leguminosae and Dipterocarpaceae in Central Africa (WATLING 1993), and with Dipterocarpaceae in Malaysia (CORNER 1972, HAWKSWORTH 1993) also suggests that the low diversity in tropical New World Boletales is anomalous.

Within the Ascomycotina, species diversity is greater at tropical latitudes among the pyrenomycetes *sensu lato* and the Xylariaceae, and possibly also at middle to low latitudes in the Melanommatales (Loculoascomycetes; Tab. 2). Previous work by DENNIS (1970) indicates that several epiphytic and parasitic leaf ascomycete groups are much more diverse at tropical than at temperate latitudes, including the Parmulariaceae, Asterinaceae, Perisporiaopsidaceae, Schizothyriaceae, Atichiaceae, Dimeriaceae, Capnodiaceae, Meliolaceae, Polytigmataceae, and the Myrangiiales. Speciation and diversity among discomycetes appears to be greater in temperate than in tropical areas, perhaps because of the more rapid decomposition of substrates in tropical climates. More species in the

Rhytismatales have been recorded in the temperate zone, but this may reflect the overwhelming number of collections from Eurasia and North America. A higher ratio of species to number of collections shows up in the Rhytismatales between 10 and 20 degrees N and S latitude, which suggests a need for greater collecting in this zone. Among hyphomycetes and plant-endophytic fungi (primarily asexual and vegetative states of ascomycetes, respectively), species diversity is generally higher at low latitudes (Tab. 2). Certain plant parasitic fungi are distinctly more diverse in the northern hemisphere than in the southern hemisphere, such as the Mastigomycotina (e.g., *Synchytrium* and *Physoderma* spp.), the downy mildews (Peronosporales: *Peronospora* spp.) and the Taphrinales (Ascomycotina) suggesting a possibly recent northern center of origin (WALKER 1983).

3.2 Altitude

Overall macrofungal and macrobasidiomycete diversity seem to be higher at middle or low elevations. Within this group, the Cortinariaceae (Agaricales) and the Boletales are most diverse at high and middle elevations (especially at tropical latitudes), whereas diversity is apparently greater at middle or low elevations in the Gasteromycetes, the Aphyllophorales (including the Polyporaceae), Neotropical Tricholomataceae (DENNIS 1970), and the Homobasidiomycetes in general (Tab. 2). There was no consensus on the relationship of elevation with overall mushroom diversity (Agaricales) in this survey, but a previous workshop on biodiversity and conservation of Neotropical montane forests concluded that the diversity of Agaricales was greater at higher elevations than at lower elevations (MUELLER and HALLING 1995). The diversity of most fungi, including the Agaricales, drops dramatically above the tree-line in the Neotropics (DENNIS 1970). No elevational patterns were noted for the Heterobasidiomycetes and related Corticiaceae.

There was a tendency for ascomycete diversity to be higher at middle to low elevations in the Melanommatales, Xylariaceae, Rhytismatales, and the broader grouping of Pyrenomycetes (Tab. 2), but the collections of Rhytismatales are biased toward countries with little topographic relief. Discomycete diversity tends to be greater at higher elevations than lower elevations in the tropics. Hyphomycetes are most diverse at low elevation. The relationship of species diversity to altitude is dependent on latitude in the Xylariaceae and plant endophytes, and probably in other fungal groups as well.

3.3 Rainfall

Diversity in almost all basidiomycetes groups (except marasmioid agarics, many of which are adapted to fluctuating humidity), was related to total annual rainfall, although seasonality of rainfall may also be important. Overall diversity in basidiomycetes Homobasidiomycetes, polypores, and macrofungi in general is apparently highest in areas of high rainfall (Tab. 2). However, certain groups such as the Aphyllophorales *sensu lato*, Boletales, Agaricales, Cortinariaceae (Agaricales), ant-garden fungi, Agaricales in the Hawaiian islands, and Tricholomataceae in the Neotropics appear to be more diverse at intermediate to high rainfall. A few groups of fungi are adapted to dry conditions and are

Tab. 2. Survey responses to questions concerning the correlates of fungal diversity (n/a means no answer or not applicable).

Taxonomic or ecological group	Fungal spp. diversity and latitude	Fungal spp. diversity and altitude	Fungal spp. diversity and rainfall	Fungal diversity and abundance	Fungal diversity and habitat diversity	Host diversity and fungal spp. diversity	Fungal diversity and resource abundance
Pyrenomycetes (Ascomycotina)	greater at low latitudes	greater at middle and low elevations	greater with constant intermediate rainfall	family, genus and species diversity increases with abundance	strongly related	somewhat related	strongly related
Xylariaceae (Ascomycotina)	greater at low latitudes	response of diversity to elevation depends on the latitude	greater with intermediate to high rain, except for some genera	no consensus; genus and spp. diversity may increase with abundance	strongly related	strongly related	strongly related
Melanommatales (Loculoascomycetes)	greater at middle to low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	family, genus and species diversity increases with abundance	somewhat to strongly related	strongly related	strongly related
Discomycetes (Ascomycotina)	higher at middle to high latitudes	greater at high elevations	greater at high rainfall	genus and species diversity increases with abundance	strongly related	strongly related	somewhat to strongly related
Rhizomatales (Ascomycotina)	possibly greater between 10 and 20 degrees	greater at middle and low elevations	greater at high rainfall	genus and species diversity increases with abundance	somewhat related	host generic div. strongly related to fungal species diversity	n/a
Hyphomycetes (mostly asexual stages of ascomycetes)	higher at low latitudes	greater at low elevations	greater at intermediate to high rainfall	genus and species diversity increases with abundance	somewhat to strongly related	strongly related	1 response of strongly related; other n/a
Agaricales (Basidiomycotina)	somewhat greater at low latitudes	no consensus	greater at intermediate to high rainfall	no relationships at any level	greatly related overall, but less strongly in Marasmius	strongly related overall	somewhat related
Entolomataceae (Agaricales)	greater at high and low latitudes	greater at high and low elevations	n/a	no relationships at any level	strongly related	strongly related	strongly related
Tricholomataceae (Agaricales)	greater at low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	species diversity is related to abundance	strongly related	somewhat related	somewhat related
Cortinariaceae (Agaricales)	greater at middle to high latitudes	greater at high to middle elevations	greater at intermediate rainfall	species diversity increases with abundance, but no consensus	strongly related	strongly related	somewhat to strongly related

Tab. 2. Continued.

Boletales (Basidiomycotina)	no consistent pattern among continents	higher at middle and low elevations	greater at intermediate rainfall	family, genus and species diversity increases with abundance	strongly related	strongly related	somewhat related
Heterobasidiomycetes and Corticiaceae (Basidiomycotina)	mixed	no pattern	greater at intermediate to low rainfall	n/a	somewhat related	strongly related	n/a
Endophytic fungi	greater at low latitudes	dependent on latitude	greater at intermediate rainfall	species diversity and abundance	strongly related	strongly related	n/a
Ant-garden fungi (Basidiomycotina)	greatest in subtropics	greater at intermediate elevation	greater at intermediate rainfall	n/a	strongly related	strongly related	strongly related
Macromycetes (Basidiomycotina)	greater at low latitudes	greater at low elevations	greater at high rainfall	species richness increases with abundance	strongly related	strongly related	strongly related
Hymenomycetes (Basidiomycotina except rusts and smuts)	greater at low latitudes	greater at middle elevations	greater at high rainfall	species richness increases with abundance	strongly related	somewhat related	strongly related
Homobasidiomycetes	higher at middle latitudes	greater at low elevations	greater at high rainfall	not related for spp.; is related for genera and families	somewhat related	somewhat related	n/a
Gasteromycetes (Basidiomycotina)	no pattern overall	greater at middle and low elevations	greater at intermediate to low rainfall	not related	little to somewhat related	somewhat correlated	somewhat related
Phallales (from lit.) (Gasteromycetes)	higher at low latitudes	n/a	greater at high rainfall	n/a	n/a	n/a	n/a
Aphyllophorales (Basidiomycotina)	higher at middle to low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	family, genus and species diversity increases with abundance	strongly related	somewhat to greatly related	somewhat related
Polyporaceae (Aphyllophorales)	higher at low latitudes	greater with decreasing elevation	greater at high rainfall	generic diversity increases with abundance	strongly related	strongly related	somewhat related

more diverse in areas with low to intermediate rainfall, such as the Gasteromycetes (excluding most stinkhorns: Phallales)(MILLER 1982), and rust and smut fungi (plant-parasitic Heterobasidiomycetes).

Among the Ascomycotina, species diversity in the Melanommatales and discomycetes is greater in areas of intermediate to high rainfall. Hyphomycetes and endophytic fungi are mostly asexual and vegetative states of ascomycetes, and follow a similar pattern (Tab. 2). In the Rhytismatales, there is a strong positive correlation of diversity with total annual rainfall in the United Kingdom. The Xylariaceae is also most diverse in areas of intermediate (2-4 m per annum in the tropics; Laessøe) to high rainfall (Rogers), but constant availability of moisture without inundation may be better than total rainfall for defining areas of high pyrenomycete diversity in general (Samuels). Some genera in the Xylariaceae are especially diverse in wet forests, such as *Xylaria* and *Camillea* (Laessøe), but other genera such as *Hypoxylon* (Whalley) and *Daldinia* (Rogers) have species that are adapted to dryer conditions.

3.4 Relationship of fungal abundance and diversity

Species diversity is not related to the abundance of fruiting bodies across all taxonomic groups, taxonomic levels, ecological groups, and geographical regions (Tab. 2). For example, positive correlations of abundance and species diversity were observed for tropical macrofungi and Hyphomycete microfungi, various orders of ascomycetes (Melanommatales, Rhytismatales, pyrenomycetes, discomycetes, and Xylariaceae) and Hymenomycetes in general, but not among tropical Homobasidiomycetes (Pegler). Abundance and species diversity were thought to be related in the Aphyllorphorales *sensu lato*, but not the Polyporaceae which is included in this group. Unpublished data from tropical wet forests show that species richness is positively correlated with the number of fructifications among Agaricales growing on leaf litter in Puerto Rico and Ecuador (Lodge and Cantrell), but not among polypore fungi on wood in Puerto Rico (Lodge, Camilo and Corbin). Certain orders and families usually show an increase in species richness with abundance, such as the Boletales and the Cortinariaceae (Agaricales), but such relationships may not hold up in all regions (e.g., Agaricales in western North America), or in certain families that fruit abundantly everywhere (e.g., Xylariaceae).

Positive correlations have been observed between abundance and diversity of basidiomycetes genera in the Aphyllorphorales including the Polyporaceae, the Boletales, Homobasidiomycetes, macrofungi in the Paleotropics, and hyphomycetous microfungi (Tab. 2). A positive relationship of abundance and diversity also appears at the family level for these groups, except the polypores. In contrast, no relationships were noted between abundance and diversity at the genus or family level in the Agaricales or the Gasteromycetes. Among the Ascomycotina, abundance is related to generic diversity in the Melanommatales, Rhytismatales, and the pyrenomycetes in general. There was no consensus on the Xylariaceae. Family diversity appears to be higher in areas of high abundance in the Melanommatales and pyrenomycetes.

3.5 Relationship of species diversity with habitat and host diversity

Species diversity of fungi in a particular geographical area appears to be strongly related to the diversity of habitats and ecosystems (13 of 17 responses for basidiomycetes and macromycetes, and seven of nine responses for ascomycetes and Hyphomycetes). However in certain groups that are adapted to dry conditions, such as the Gasteromycetes, or periodic desiccation, such as the marasmioid agarics, species diversity is less strongly related to habitat or ecosystem diversity (Tab. 2).

Species diversity among basidiomycetes and ascomycetes is also strongly related to host diversity (12 out of 15, and 10 out of 11 responses, respectively). Species richness is apparently less strongly related to host diversity in large, inclusive groups that contain many decomposers, such as the Hymenomycetes, Homobasidiomycetes in general, the Aphyllaphorales s./., and the Gasteromycetes (Tab. 2). However, even in genera composed primarily of decomposers, such as *Marasmius*, species diversity can be strongly related to the diversity of hosts. Similarly, species diversity in discomycetes (Ascomycotina) and Hyphomycetes is a strongly related to host diversity (Tab. 2) although these groups are dominated by decomposers. Specificity of decomposer *Xylaria* spp. for particular host genera or families also occurs (LAESSØE and LODGE 1994). Species richness is more closely related to host plant diversity at the genus rather than the species level in the parasitic Rhytismatales and probably in other fungal groups as well.

3.6 Species diversity and resource abundance

Only five of the responses for basidiomycetes indicated that resource abundance was greatly related to species diversity (Tab. 2). Resource abundance may be relatively more important for fungal diversity in groups that include many decomposers, such as the Agaricales, Entolomataceae, Hymenomycetes and macrofungi in general, but only one author (Petersen) felt it was more important than host diversity. The relationship between species richness and abundance of resources may be generally stronger among ascomycete and hyphomycete groups that are dominated by decomposers.

3.7 Areas with high diversity

Five of the six authors with experience in both the Neo- and Paleotropics ranked the Neotropics, especially the Amazon basin, as having the greatest diversity of Aphyllaphorales, pyrenomycetes, Xylariaceae, and hyphomycetes. The exception was Homobasidiomycetes in the Lesser Antilles, a chain of small islands in the southern Caribbean (Pegler). The Neotropics have a higher diversity than Africa of hyphomycetes and xylariaceous ascomycetes (WHALLEY 1993). Subtropical and temperate South America were ranked higher in diversity of Cortinariaceae than New Zealand, Australia and New Guinea, but lower than those countries in diversity of Entolomataceae (Agaricales: HORAK 1976, 1979, 1980, 1982; MOSER and HORAK 1975). Subtropical São Paulo State in Brazil was also thought to have a lower diversity of Homobasidiomycetes than Africa, India, Sri Lanka, or Malaysia. Africa has a high diversity of macromycetes in general (WATLING

1993), polypores (RYVARDEN 1993), and hyphomycetes. India, tropical Nepal, and the Chinese and Asian tropics may also have high diversities of fungi. but our knowledge of these areas is limited. Except for the Gasteromycetes. Europe always had the lowest diversity of fungi when it was included in the rankings (six responses). However, a previous survey by WALKER (1983) indicates that the downy mildews (Peronosporales) are most diverse in Europe.

3.8 Species with restricted distributions

Two geographically isolated areas that were most frequently noted as having species restricted to the region were Australia (especially Queensland: Boletales, Gasteromycetes, Cortinariaceae, Entolomataceae, and Xylariaceae), and New Zealand (Hymenomycetes, Cortinariaceae, pyrenomycetes, Rhytismatales and discomycetes). New Guinea was also mentioned as having species of Entolomataceae (HORAK 1980) and discomycetes that have not as yet been found elsewhere. Species in the Gasteromycetes that are dispersed by flies (DRING 1980) or rodents (FOGEL 1994) often have very restricted distributions. Although gasteromycete species with airborne spores generally have very wide distributions, 56% of 183 species of Gasteromycetes that have been reported from Australia and New Zealand are endemic. Various parts of Africa were noted to have apparently unique species, e.g., species of Xylariaceae in parts of Ethiopia and the Congo basin (WHALLEY 1993), Polyporaceae in Miombo forest in South-Central Africa, and more generally, Heterobasidiomycetes (OBERWINKLER 1993) and Homobasidiomycetes in various parts of Africa. In the Western Hemisphere, unique species of Xylariaceae and Tricholomataceae are frequent in the western Amazon basin. Although species with restricted ranges appear to be the rule rather than the exception in the Agaricales, they may be especially prevalent in temperate habitats on mountaintops at tropical latitudes such as in Central America and the Andes of South America, and on islands such as those in the Caribbean and the Pacific. The knowledge of agaric mycotas in the Caribbean and Hawaiian islands and their neighboring regions is currently too fragmentary to draw conclusions about endemism, however. In addition to Australia, the South-Eastern United States has a high number of endemic Boletales. Some species of Rhytismatales are restricted to mountaintops in Greece, but this group and other parasitic fungi including many Heterobasidiomycetes (WALKER 1983, OBERWINKLER 1993) have species with restricted ranges in many parts of the world. Some species of the primarily saprotrophic Melanommatales are known to have widespread distributions. Similarly, no centers of endemism were noted for hyphomycetes.

4 Discussion

As in higher plants and many animal groups, the diversity of fungi in the Hymenomycetes (Basidiomycotina, excluding rusts and smuts) and the Ascomycotina overall appears to be greatest in the tropics and subtropics. This pattern may not be directly related to the climatic correlates of latitude. For example, fungi may be most diverse in the tropics because the diversity of host plants and invertebrates is greatest in the tropics. The tropics

might also represent refugia for many taxa, including fungi. Total land area is greater at low than at high latitudes (TERBORGH 1977), a pattern that is likely to contribute to greater species richness in the tropics. Furthermore, the distances between continents are greater at tropical latitudes than at Cool-Temperate and Boreal latitudes, and this isolation may contribute to greater speciation in the tropics.

Most groups of fungi included in this survey reach their maximum diversity at intermediate to low elevation, suggesting a relationship with climate, but species/area relationships may contribute to this pattern. Area on the tops of mountains is very limited, and this may restrict the number of species that are adapted to temperate forests and paramos on the tops of mountains at tropical latitudes (TERBORGH 1977). Host diversity may also contribute to elevational gradients in fungal diversity because potential host plants and invertebrates reach their highest diversities at middle to low elevation. The ranges of taxonomic groups that are more diverse at high elevations, such as the Cortinariaceae (Agaricales), and the ranges of groups that are more diverse at lower elevations overlap at intermediate altitudes, possibly contributing to the high diversity in this zone. There was no consensus on the relationship of elevation with mushroom diversity (Agaricales). This may reflect a weak pattern, mixed patterns for different groups or an insufficiency of data. For example, some of the most speciose genera in the Agaricales (e.g., *Inocybe*, *Russula*, and *Cortinarius* with more than 2,000 spp. alone) are ectomycorrhizal associates of trees in certain plant families, and their diversity follows the abundance and diversity of their hosts. Consequently, there is a great diversity of ectomycorrhizal fungi in *Quercus* forests at intermediate to high elevations in Central America and Colombia and in association with Pinaceae in Mexico and northern Central America (MUELLER and HALLING 1995), as well as at low elevations in association with Leguminosae and Myrtaceae in Africa (WATLING 1983), and at various elevations in association with Dipterocarpaceae in Malaysia.

Almost all of the published literature on endangered species of non-lichenized fungi relates to the diversity of macrofungi in Europe, especially mycorrhizal symbionts (e.g. FELLNER 1983, 1988, 1989, 1993; ARNOLDS 1988, 1991; DERBSCH and SCHMITT 1987; JAKUCS 1988; NAUTA and VELLINGA 1993). On a global scale, however, Europe has the lowest diversity of ectomycorrhizal basidiomycetes and many other fungal groups, so efforts to conserve global biodiversity will have to include many areas in the tropics that have a much higher fungal diversity, but have been poorly surveyed in the past. The rates of tropical deforestation are high, so rapid inventory and classification techniques are needed to identify areas having the highest diversity and greatest numbers of unique fungal species, genera and families for conservation (HAWKSWORTH 1993). For example, if a positive relationship exists between the abundance of fructifications and the diversity of fungi, then initial surveying of regions for areas of high diversity could be done by trained technicians rather than fungal taxonomists. Although positive correlations occur, such an approach is not likely to work across all taxonomic groups, ecological groups, or biomes, and in some cases may not be strong enough to be useful. For example, some genera that are tolerant of dryer conditions, such as *Hypoxylon*, fruit abundantly more or less everywhere and this may weaken the relationship of fruiting abundance and species diversity in the Xylariaceae. Most of the genera and families in the Agaricales are widely distributed, which may explain the absence of a relationship between abundance and diversity above the species level in this order.

In a recent book on biodiversity, an ecologist (HUSTON 1994) hypothesized that detrital and decomposer communities would reach their highest diversity where plant productivity was highest, independent of plant diversity. The results of this survey suggest that HUSTON'S (1994) hypothesis may not be correct. Only five authors felt that resource abundance was greatly related to species diversity in their basidiomycetes group as compared to 12 authors who felt there was a strong relationship with host diversity. The relationship between species richness and abundance of resources maybe somewhat stronger in groups such as the ascomycetes that are dominated by decomposers, but many decomposers are also host-specific to some degree. It is important for mycologists to test ecological hypotheses such as the one by HUSTON (1994) because they are likely to influence conservation policies in the absence of quantitative data on fungal diversity.

The Neotropics have a very high fungal diversity, and the Amazon basin may have a higher diversity of Xylariaceae and hyphomycetes than Africa. One possible explanation is that diversity in these fungal groups is apparently related to host diversity, and the diversity of higher plants is greater in the Neotropics than in Africa. Some genera, such as *Camillea* (Xylariaceae: LAESSØE *et al.* 1989; WHALLEY 1993) are found almost exclusively in the New World, which might indicate a diversification of this group after the continents parted, but almost nothing is known about vicariance biogeography in fungi. Alternatively, the limited extent of wet forests, and the waves of drought that have historically passed through Africa and are thought to have limited plant diversity (GARTLAN 1974) may have also reduced fungal diversity. The authors familiar with Africa and Asia suggest, however, that these areas are undersampled and in need of more collecting, so comparisons between continents are premature. Comparable surveys of fungi (using the same observers, methods, and sampling areas) in forest ecosystems on different continents, in which the study areas have been carefully paired for climate, would be more useful for addressing broad geographical patterns in fungal diversity than the ad hoc comparisons presented here.

There is some evidence cited in the ecological literature for long-distance dispersal of viable spores in the jet-stream (CARLQUIST 1965) that has led to a misconception that fungi are able to disperse everywhere. Although some species of polypores (RYVARDEN 1993) and Heterobasidiomycetes (OBERWINKLER 1993), and probably most species of Gasteromycetes, hyphomycetes, and Loculoascomycetes are widely distributed, other species and groups of fungi apparently have restricted geographic ranges. The ranges of some tropical species may not be as restricted as they appear because of the lack of adequate surveys; some species of ascomycetes and basidiomycetes that were once thought to be very restricted have later been found on other continents (OBERWINKLER 1993; WATLING 1993; WHALLEY 1993). The limited ranges of some fungal species (e.g., parasitic Heterobasidiomycetes and ascomycetes, and agaric fungi of ant-gardens) may be explained by the limited ranges of their hosts, while the distribution of others may indicate a recent origin. The common and widespread occurrence of species with limited ranges among the Agaricales, however, suggests that other factors such as intersterility or limited colonization potentials may be involved. For example, incompatibility between certain closely related mushroom taxa within continents and between Europe and North America indicates the presence of sibling species with geographically restricted ranges rather than one widely distributed species (PETERSEN 1995). There is little overlap of *Laccaria* species among regions (MUELLER 1992) and intersterility among related species is

common in the *L. laccata* and *L. bicolor* complexes (FRIES and MUELLER 1984; MUELLER 1991, 1992). Other examples of incompatibility among sympatric or allopatric populations of Agaricales include species of *Marasmius*, *Oudemansiella*, and possibly *Armillaria*, and *Marasmiellus praeacutus*. Incompatibility is also found among some polypore fungi, such as *Fomitopsis pinicola* and the more ephemeral species of *Pleurotus* and *Polyporus* (*sensu stricto*), and among ascomycetes in *Nectria* and *Gibberella*.

Taxonomic groups can exhibit different degrees of reduced diversity on islands with increasing geographic isolation (disharmony; CARLQUIST 1965) because of differences in their means of dispersal, sensitivity to environmental stress, or reproductive biology. For example, successful dispersal might be limited in agarics that have thin-walled spores because of their susceptibility to desiccation. This could help explain the disparity between the limited distributions that are prevalent in the Agaricales, and the widespread distributions of species of Gasteromycetes that are adapted to dry conditions (e.g. *Podaxis* spp.). Regional diversity in lineages with good dispersal is sometimes less than in lineages with poorer dispersal because lack of reproductive isolation among populations can reduce speciation (RICKLEFS and COX 1972), but little is known about the relationship of dispersal and speciation in fungi.

Monokaryotic and dikaryotic mycelia of basidiomycetes frequently have different growth characteristics (GUILLAUMIN *et al.* 1991; MUELLER 1991; PETERSEN and BERMUDEZ 1992; LARSEN *et al.* 1994; PETERSEN 1995) but the significance of this to colonization and competitive abilities is unknown. However, in the Agaricales, the low probability of landing near enough to an opposite mating type to result in dikaryotization and subsequent sexual reproduction may favor colonization of islands or habitat islands by vegetative structures (fungi of ant-gardens) or asexual, homokaryotic or otherwise self-fertile spores (Homobasidiomycetes). This might lead to increased founder effects, reproductive isolation, and speciation of basidiomycetes on islands or in habitat islands in Agaricales, but dikaryon matings with monokaryons via the Buller phenomenon may provide gene flow among some populations (EGGER 1995). For example, DEACON and FLEMING (1992) suggest that while colonizing (ruderal) species of mycorrhizal fungi are more likely to become established as monokaryons, late stage species require substances produced by an established mycelium in order to break spore dormancy. If this pattern occurs among basidiomycetes in general, it could help explain differences between widespread and geographically restricted species.

5 Conclusions

Although the data on fungal diversity and distributions are limited and fragmentary, the consensus of opinions suggests that certain patterns are robust and are worthy of further pursuit and testing. Diversity in many fungal groups is apparently greatest at low or middle to low latitudes, intermediate to low altitude (except Agaricales and Heterobasidiomycetes), and intermediate to high rainfall. Species with restricted ranges are frequently more abundant on islands or in habitat islands, temperate habitats on top of tropical mountains, and in large expanses of tropical rain forest. Such patterns of limited distribution in fungi coincide with those of many plant and animal groups. Groups that have widespread species are often adapted to harsh conditions, and consist mainly of de-

composers. Fungal diversity seems to be related most strongly to habitat and host diversity (especially among parasites and mutualists, but also among some decomposers), although the abundance of resources might also be important in certain groups. In addition to parasitic fungi, species with limited ranges are common among the Agaricales. Certain mating and incompatibility systems and the susceptibility of spores to desiccation in some genera may contribute to this pattern.

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