Host Specialization among Wood-Decay Polypore Fungi in a Caribbean Mangrove Forest[1]

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ABSTRACT

Host specialization in highly diverse tropical forests may be limited by the low local abundance of suitable hosts. To address whether or not fungi in a low-diversity tropical forest were released from this restriction, fruiting bodies of polypore basidiomycete fungi were collected from three species of mangroves (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) in a Caribbean mangrove forest in Panama. Unlike other tropical forests, the polypore assemblage in this mangrove forest was strongly dominated by a few host-specialized species. Three fungal species, each with strong preference for a different mangrove host species, comprised 88 percent of all fungi collected.

RESUMEN

En los bosques tropicales de alta diversidad, la especialización por un hospedero particular puede verse limitada debido a la baja abundancia de hospederos apropiados. Para determinar si dicha limitación de hospederos no ocurre en los hongos que crecen en bosques tropicales de baja diversidad, se recolectaron cuerpos fructíferos de hongos basidiomicetos poliporoides presentes en tres especies de mangle (*Avicennia germinans*, *Laguncularia racemosa*, y *Rhizophora mangle*) en un manglar de la costa caribeña de Panamá. A diferencia de otros bosques tropicales, la comunidad de hongos poliporales en el manglar estudiado se encontraba dominada por pocas especies altamente específicas. Tres especies de hongos, cada una con una preferencia particular por un hospedero diferente, representaron el 88 por ciento de todos los hongos recolectados.

ESTIMATES OF FUNGAL DIVERSITY VARY WIDELY; extrapolations from the 72,000 species currently described range as high as 9.9 million (May 1991; Aptroot 1997; Cannon 1997a, b; Lodge 1997; Fröhlich & Hyde 1999; Zhou & Hyde 2001), with the most commonly cited estimate of 1.5 million (Hawksworth 1991). These estimates of global fungal diversity are based on the perception that most species have yet to be described (estimated as only 1 to 20% for fungi) and on an estimated ratio of fungal to plant species in specified areas (Hawksworth 1991, Rossman 1994). For tropical forest systems in particular, it is clear that the current number of described fungal species is only a small fraction of the number of species that exist there (Rossman 1994; Fröhlich & Hyde 1999; Arnold *et*

al. 2000, 2001). Refining the estimates of global fungal richness will require a better understanding of the constancy of the plant to fungus ratio across different geographic regions and ecosystem types (Huhndorf & Lodge 1997). Additionally, global diversity estimates could be improved by a better understanding of what proportion of the fungal biota is particularly associated with plant material, and among those, how relative specificity varies among fungi that infect different parts of live or dead plants (see recent review in Zhou & Hyde 2001). If tropical fungi that infect plants show strong preferences for particular hosts, then the high diversity of plants in tropical forests suggests extremely high tropical fungal diversity. May (1991), however, has suggested that high-diversity tropical systems may support less host specificity than low-diversity systems due to the low density of individual host species and the limitation this places on colonization of suitable substrates and

therefore on the persistence of fungal populations that are host-specific. Understanding the processes that determine the scope and maintenance of tropical biological diversity requires an appreciation of the structure and specificity of plant-dependent organisms such as fungi in both high- and low-diversity forests.

Several recent studies have provided conflicting data on levels of host specificity among fungi in diverse tropical forests. Arnold *et al.* (2000, 2001) found evidence for host preference in a study of leaf-inhabiting microfungi of two shrub species in a lowland moist tropical forest in Panama, finding 62 percent of non-singleton taxa restricted to one host or the other. Similar results were found by Polishook *et al.* (1996) for microfungi in decaying leaves of two tree species that were mixed together on the forest floor in Puerto Rico. In contrast, two studies showed little evidence of host preferences among wood-decay polypore fungi in a seasonally dry tropical forest (Lindblad 2000) and in a lowland moist forest (Gilbert *et al.* 2002a). Similar low host specificity was found for wood-inhabiting Ascomycetes in a subtropical wet forest in Puerto Rico (Huhndorf & Lodge 1997). Critical to improving our understanding of the scope and structure of fungal diversity is recognizing that fungi exhibit a diversity of fungal life history strategies, and that levels of host preferences may vary greatly among different ecologically or phylogenetically defined groups of fungi.

If fungal host specificity were limited by the availability of suitable hosts, then we would expect the fungi of low-diversity tropical forests to exhibit a greater level of host preference than those of high-diversity tropical forests. Among tropical forests, mangroves are particularly noteworthy for their low species diversity and relatively high density of trees, with Neotropical mangrove forests comprised generally of only three to four tree species (Tomlinson 1986). Such forests grow in tidally inundated soil along tropical and subtropical coastlines, occupying the depositional environments that salt marshes dominate at higher latitudes. The stressful edaphic environments in which mangroves live and reproduce greatly limit plant diversity. We expect therefore that mangrove forests would support a substantially specialized polypore flora, in addition to more generalist species. Such specialists could be either global mangrove specialists or locally adapted and specialized varieties of globally generalist species (Thompson 1994).

Our present knowledge of the levels of host specificity among fungi in mangrove forests is lim-ited. Ascomycete marine fungi that grow on intertidal portions of mangrove stems and roots, and on decomposing leaves and woody material, are the best studied fungi in this habitat (reviews in Hyde 1988, Hyde & Jones 1988, Hyde & Lee 1995, Jones & Alias 1997). These fungi tolerate the saline, frequently anoxic, and intermittently flooded conditions characteristic of the intertidal zone in mangrove habitats. As with most intertidal fungi, those associated with mangroves are generally pantropical, and few species show strong host preferences (Hyde & Lee 1995). Hyde (1990), however, found evidence for host preferences among 75 species of Ascomycetes and 1 species of Basidiomycetes growing on mangrove wood in Brunei, with dominant fungi differing across the five host mangrove species.

Nearly unstudied is the host specialization of polypore basidiomycete fungi that act as pathogens or wood decayers in live or standing-dead mangrove trees. Polypore fungi belong to several orders within the Basidiomycetes, but are ecologically grouped by being restricted to a single, clearly defined substrate (wood of living or dead trees) and through their similar reproductive biology characterized by airborne sexual basidiospores produced in large, persistent fruiting bodies. Among the polypores are fungi that are primary pathogens of healthy trees and others that apparently only infect deadwood, but many species cross over through many stages of the host plant, infecting living trees, decaying deadwood within live trees, and continuing to decompose deadwood. Their unifying attributes, relatively well-known taxonomy, persistent fruiting bodies, and abundance in mangrove forests above the tidal line make the polypore fungi a well-defined natural ecological group for the study of host specialization in mangrove forests.

Tropical forests support a rich diversity of polypore fungi, with the diversity of polypores outstripping that of trees even in diverse lowland moist tropical forests (Carranza 1996, Gilbert *et al.* 2002a). On Maracá Island off the Caribbean coast of Brazil, Sotão *et al.* (1991) reported 23 species of polypore fungi collected from decomposing trunks and roots of *Rhizophora* (Rhizophoraceae) and *Avicennia* (Avicenniaceae), but they did not determine the hosts from which the fungi were collected. Based on herbarium specimens collected from coastal mangroves in São Paulo, Brazil, Almeida Filho *et al.* (1993) reported three polypore species on *Laguncularia racemosa* (Combretaceae), one on *Tabebuia cassinoides* (Bignoniaceae), one on *Rhizophora mangle*, and three on unidentified mangroves.

Neither study provided information on relative abundance or host preferences for the fungi described.

To begin assessing the structure and diversity of the wood-decay fungal community associated with mangrove forests and to test the hypothesis that fungi should be more host specialized within a mangrove forest than in more diverse forests, we made systematic collections of all fruiting bodies of polypore fungi along three transects from open saltwater to upland sites in a Caribbean mangrove forest in central Panama. We quantified the diversity of fungi on each of the three host species, compared the assemblage of polypores in the mangrove forest to that in adjacent, more diverse upland forests, and examined the importance of host specificity in structuring the local fungal community.

MATERIALS AND METHODS

STUDY SITE AND FOREST COMPOSITION.—The study was conducted in mainland mangrove forests near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory (9°24′18″N, 79°51′48.5″W) at Punta Galeta on the Caribbean coast of Panama, *ca* 8 km northeast of the city of Colón (see Fig. 1 in Sousa & Mitchell 1999). Three tree species comprise the canopy of the study forests: *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and *Rhizophora mangle* (red mangrove; hereafter referred to by their generic names). In these forests as elsewhere (Davis 1940, Schaeffer-Novelli *et al.* 1990, McKee 1995, Imbert & Ménard 1997, Sherman *et al.* 2000), these species are distributed differentially with distance from the water's edge, but their distributions overlap to varying degrees (W. Sousa & B. Mitchell, pers. obs.). In our study forests, *Rhizophora* forms a pure or nearly pure stand in the low intertidal zone, within 10 to 20 m of the water's edge. The forest then changes to a more even mixture of *Rhizophora* and *Laguncularia*, which extends landward for another 40 to 180 m before adult *Avicennia* appear in the canopy. In another 30 to 70 m, *Rhizophora* drops out, and above that point, in most areas, *Avicennia* gradually monopolizes the canopy. *Laguncularia* may disappear completely from the canopy 20–40 m above the upper limit of *Rhizophora*, or it may occur only as scattered individuals. Local variations in this general pattern, however, are common.

FUNGAL COLLECTION.—Fungi were collected during 19–22 July 1995, along three 10 m wide belt transects running from the water's edge to the lower edge of upland rain forest vegetation. The transects were 230 (Pipeline), 270 (Bahia Margarita), and 310 m (Minas Sur) long, and positioned to encompass the range of forest settings within the study area. One transect originated on the edge of an estuarine lagoon, another at the edge of an open oceanic bay, and the third from the bank of a small, tidally influenced river. They were established in 1994 within areas of mature, closed canopy forest. In each 10 × 10 m section of a transect, we identified and measured the diameter at breast height (DBH) of all trees 4 cm or greater (both living and dead). Because the three tree species in Caribbean mangrove forests are morphologically quite distinctive, it is possible to identify trunks to species, even when trunks are in relatively advanced stages of decay.

All fruiting bodies (basidiomata) of polypore fungi (orders Ganodermatales, Hymenochaetales, Poriales, and Stereales) encountered along the three transects were collected and air-dried. Collections were restricted to polypore fungi because the fruiting bodies are macroscopic and persistent (lasting months to years), the taxonomy is better known than for other groups of tropical fungi, and because of their importance in wood decay and tree diseases. The collections included "polypore" fungi without true pores. Nonreproductive polypores may have gone undetected during this study, but subsequent collecting from this and other sites in Panama at various times of the year indicate that the collection represents the major components of the polypore assemblage (Gilbert, Parrent, and Garbelotto, pers. obs.). Multiple basidiomata of the same species growing on an individual tree or log were considered one collection. Fungal samples were identified using standard macro- and micromorphological characteristics (Ryvarden & Johansen 1980, Gilbertson & Ryvarden 1986) and through comparison with herbarium materials. We are indebted to María Nuñez, University of Oslo, for identifying or confirming the identifications of representative samples of all species. Voucher samples have been deposited with the herbaria at the University of Panama and the University of California, Berkeley.

In addition to the three transects, we collected all polypore fungi from upland areas with non-mangrove forests at the inland end of each transect. These areas are essentially higher elevation islands or peninsulas of rain forest habitat surrounded by mangrove stands. Instead of sampling along transects through these sites, three people walked sys-

tematically across the hills, collecting all fungi encountered. We searched *ca* 3000 m² in each site, an area comparable to that of the transects. Because of the high diversity of host species (at least 50 spp./ha), it was not possible to identify upland forest hosts in many cases, particularly the specific identities of dead trees and logs; however, no mangrove species were found in those areas.

ANALYSES.—To test for host selectivity among the fungi, we used the transformation module in Systat, ver. 8.0 to calculate the binomial probability of observing "≥" the recorded number of basidiomata of a particular fungus found on its most commonly used host tree species, given the available distribution of hosts. The expected distribution of collections among the three host species, assuming no host preference, was estimated from combined counts of living and dead trees along the three transects (264 *Avicennia*, 973 *Rhizophora*, and 315 *Laguncularia* trunks). Sample sizes of fungi were too small to reliably test host preferences for each transect separately.

RESULTS

We collected 115 fruiting bodies of pore fungi from the three transects through the mangrove forest. The collection comprised nine species: five species of *Phellinus* (Hymenochaetales) and four species representing different genera of Poriales (Table 1). Nearly half (4/9) of the species were found only once; however, three species, *Datronia caperata*, *Phellinus swieteniae*, and *Trichaptum biforme* together constituted 87.8 percent of the collections (Table 1). All five species that were found multiple times showed strong host preferences, each being found exclusively (or nearly so) on only one of the three mangrove host species (Table 2). *Ceriporiopsis aneinira* was found only four times, always on *Rhizophora*, but this frequency was too low for a meaningful statistical test of preference.

From the upland areas of non-mangrove forest, we collected 25 fruiting bodies comprising 15 species of polypore fungi at the three sites (Table 3). Only two species, *D. caperata* (three collections) and *Phellinus gilvus* (five collections), were found in common between the mangrove and upland sites. The other two dominant fungi from the mangrove collections, *P. swieteniae* and *T. biforme*, were absent from the adjacent upland sites.

There were some differences in the substrates exploited by different species of fungi in the mangrove forest (Table 4). *Phellinus swieteniae*, restrict-

TABLE 1. *Frequency of collection for all species of pore fungi (Poriales and Hymenochaetales) from black (Avicennia germinans), red (Rhizophora mangle), and white (Laguncularia racemosa) mangroves in three transects at Punta Galeta, Panama. Shown at the bottom are the total number of live and dead individuals for each host species in the transects.*

Fungus	Bahia Margarita			Minas Sur			Pipeline			
	Black	Red	White	Black	Red	White	Black	Red	White	Total
Phellinus swieteniae (Murrill) S. Herrera & Bondartseva	26	0	0	10	0	0	12	0	0	48
Trichaptum biforme (Fr. in Klotzsch) Ryvarden	1	7	1	0	14	0	0	4	0	27
Datronia (= *Coriolopsis*) *caperata* (Berk.) Ryvarden	0	1	10	0	0	9	0	0	6	26
Phellinus adhaerens J.E. Wright & Blumenf.	0	0	1	0	0	3	0	0	2	6
Ceriporiopsis aneinira (Sommerf.) Domanski	0	2	0	0	1	0	0	1	0	4
Ceriporia alachuana (Murrill) Hallenb.	0	0	0	0	0	0	1	0	0	1
Phellinus callimorphus (Lev.) Ryvarden	0	0	0	0	0	0	0	0	1	1
P. gilvus (Schwein: Fr.) Pat.	0	1	0	0	0	0	0	0	0	1
Phellinus sp.	0	0	1	0	0	0	0	0	0	1
Total fungal collections	27	11	13	10	15	12	13	5	9	115
Number of live hosts	98	75	48	46	725	118	46	52	77	
Number of dead hosts	48	24	32	10	77	7	16	20	33	

TABLE 2.   *Host preference for the five species of pore fungi found more than one time in the mangrove forest (all three transects combined). Entries include the number of times a particular fungal species was collected from the dead or living trunks of each of the three mangrove species and the binomial probability of observing ≥ the recorded number of infections by a particular fungus of its most commonly used host tree species. The patterns for four of the five species showed strong evidence of host specificity. The data strongly suggested a similar conclusion for the fifth species (*Ceriporiopsis aneinira*), which was only found on* Rhizophora mangle, *but the small number of collections (*N = 4) *precluded meaningful statistical testing for host specificity in this case.*

| | Mangrove host | | | |
| | *Avicennia germinans* | *Rhizophora mangle* | *Laguncularia racemosa* | *P*-value |
Fungus				
Phellinus swieteniae	48	0	0	<0.0001
Trichaptum biforme	1	25	1	0.0005
Datronia caperata	0	1	25	<0.0001
Phellinus adhaerens	0	0	6	<0.0001
Ceriporiopsis aneinira	0	4	0	—

ed to *Avicennia*, was mostly found on live trees. This species aggressively attacks live hosts, hollowing the trunks of many of the larger individuals. Such heart rot was not seen in other host species. In contrast, *T. biforme* was restricted to dead trunks and a few dead branches on live trees. *Datronia caperata* exhibited an intermediate pattern; it was found on the trunks of live trees, dead branches, and standing, recently dead trunks.

DISCUSSION

The polypore mycoflora of the Caribbean mangrove forest at Punta Galeta was dominated by a few common species with strong host preferences. This differs greatly from reports from other tropical forests, where most polypore species are rare and more common species are host generalists (Lind-blad 2000, Gilbert *et al.* 2002a). The strong dominance by a few host-restricted polypore fungi also far exceeds that seen in low-diversity temperate forests (Bader *et al.* 1995, Renvall 1995). None of the polypore species sampled in the mangrove forest are mangrove specialists, all described in the literature as being from non-mangrove hosts (Ryvarden & Johansen 1980, Wright & Blumenfeld 1984, Gilbertson & Ryvarden 1986, Job & Rajchenberg 1988); however, within the local community context, there is strong support for specialization on particular mangrove hosts.

The only directly comparable data on the diversity and specificity of fungi across mangrove hosts come from Hyde's 1990 study of intertidal fungi on five mangrove species in Brunei, which focused almost exclusively on Ascomycetes. Most taxa in that collection were rare, with 67 percent

TABLE 3.   *Number of collections of all species of pore fungi (Ganodermatales, Hymenochaetales, Poriales, and Stereales) found in 3000 m² surveys in upland areas of non-mangrove forest.*

Fungus	Bahia Margarita	Minas Sur	Pipeline
Datronia caperata (Berk.) Ryvarden	1	0	2
Ganoderma lucidum (Curtis: Fr.) Karst.	0	1	0
Grammothele fuligo (Berk. & Broome) Ryvarden	1	0	1
Hexagonia papyracea Berk.	0	0	1
Hymenochaete tabacina (Sowerby ex. Fr.) Lev.	1	0	0
Loweporus tephroporus (Mont.) Ryvarden	0	1	0
Phellinus gilvus (Schwein: Fr.) Pat.	1	1	3
P. palmicola (Berk. & M. A. Curtis) Ryvarden	0	0	1
Phellinus sp. 1	0	0	1
Phellinus sp. 2	2	0	0
Phellinus sp. 3	1	0	1
Polyporus grammocephalus Berk.	1	0	0
Rigidoporus microporus (Fr.) Overeem	1	0	0
Schizopora flavipora (Cooke) Ryvarden	0	0	1
Trametes lactina (Berk.) Pat.	1	0	0

TABLE 4. *Substrate distribution for polypore fungi on mangroves at Punta Galeta, Panama.*

	Number of collections from each substrate type			
Fungus	Live tree	Dead branch on live tree	Dead standing trunk	Dead fallen trunk
Phellinus swieteniae	30	1	8	9
Trichaptum biforme	—	4	14	9
Datronia caperata	2	5	19	—
Phellinus adhaerens	3	—	3	—
Ceriporiopsis aneinira	—	—	1	3
Ceriporia alachuana	—	—	—	1
Phellinus callimorphus	—	—	1	—
P. gilvus	—	—	1	—
Phellinus sp.	—	—	—	1

of the 76 species each found in fewer than 2 percent of the wood samples (and ≤1.2% of the fungal isolates). This pattern of many rare species and no strongly dominant species is similar to studies on other tropical fungal communities (Tan & Leong 1992; Bills & Polishook 1994; Polishook *et al.* 1996; Huhndorf & Lodge 1997; Arnold *et al.* 2000, 2001; Lindblad 2000; Gilbert *et al.* 2002a) and communities of fungi in general (Crawford *et al.* 1990, Espinosa-Garcia & Langenheim 1990, Fisher & Petrini 1990, Durall & Parkinson 1991, Bader *et al.* 1995, Renvall 1995). Hyde (1990) suggested that some species of intertidal mangrove fungi in his collections showed strong host preferences, while others did not; however, he presented no statistical analysis. To evaluate his conclusions, we applied the binomial test procedure described earlier (see Methods) to the frequency data in Hyde's (1990) Table 1. For each of the 76 fungal species, we tested if the number of isolates observed on the most frequently used host was greater than one would expect by chance ($P = 0.05$). Our analysis has one major caveat. Hyde (1990) selected a nonrandom sample of 100 deadwood samples from each of the five tree species, from which he incubated the fungi. While his haphazard samples are unlikely to be badly biased with respect to the kinds of fungi growing in each type of wood, we do not know the relative contributions of the five mangrove species to deadwood in his study forests. Therefore, we cannot calculate the true expected proportions of each host substrate available for fungal colonization. Instead, we have had to substitute the relative abundances of the wood types in Hyde's (1990) collection, which are 0.20 (100/500) in each case. For this reason, our analysis should be interpreted with caution, although we believe the general patterns we found are correct.

The binomial tests indicated that 77 percent of the 66 testable fungal taxa (those present two or more times in the collection) showed a significant degree of host selectivity, infecting their most commonly used host species more frequently than expected by chance. The two most abundant fungal species, however, were each found in only 13 percent of the wood samples, and both were found on all five mangrove hosts. Among the 15 most common fungal species (each representing more than 2% of the fungal collection), all but 2 were found on multiple host genera. The two exceptions were restricted to the genus *Rhizophora*, but they were found on both the *Rhizophora* species studied. Intertidal mangrove fungi appear to have some degree of preferences among their local hosts but do not approach the extreme specialization we found for polypore fungi.

If the degree of host specificity is a function of local host density, one would also expect the fungi of low-diversity temperate forests to exhibit a relatively high degree of host preference. The limited data available partially support this prediction. Renvall (1995) found 166 species of wood-inhabiting Basidiomycetes (including polypores and more ephemeral Basidiomycetes such as agarics) on fallen trunks of *Picea abies* and *Pinus sylvestris* in Finland, with 66 percent of the species found in 1 percent or less of the samples. The most common species was found on fewer than 11 percent of the trunks and represented only 4.3 percent of the fungal collections. The 20 most common species comprised only 52 percent of the fungal collection; this lack of dominance and large number of rare species in the fungal community is much more similar to that found in dry and moist lowland tropical fungi (Lindblad 2000, Gilbert *et al.* 2002a) than to the mangrove fungal community with very strong dominance. On the other hand, of the 35 fungal species Renvall (1995) found 20 or more times, 12

(34%) were restricted to only one of the two host species; a strong pattern of host preference was not seen in the high-diversity tropical forests but was very strong in the low-diversity mangrove forest.

Remarkably similar patterns of variation in host-use specialization as a function of local host plant diversity and density have been observed in mistletoes (Barlow 1992, Norton & Carpenter 1998), the largest group of angiosperm shoot parasites. Loranthaceous mistletoes show low host specificity in diverse tropical rain forests but high host specificity in low-diversity temperate forests, open and arid tropical woodlands, and mangrove forests.

The fungi described here may be important in the dynamics of the mangrove forest. In particular, *P. swieteniae* was most commonly associated with live, hollowed out trees. Such damage may subject *Avicennia* to windthrow in storms or to secondary attack by other pathogens or insects. Further study of the epidemiology and impact of these fungi on the mangrove community is needed. Similarly, the consistency of association of these fungi in other mangrove forests needs to be addressed; preliminary studies at various times of the year indicate that the three dominant fungal taxa also dominate the mycoflora in mangrove forests on both the Caribbean and Pacific coasts of Panama (Gilbert, Parrent, and Garbelotto, pers. obs.).

It would be particularly interesting to explore the interactions between environmental factors and physiological characteristics of mangrove host species in determining host specialization of these polypore fungi. The hosts themselves are zonated, with different species dominating according to increasing distance from the open ocean. Fungi in our study were nearly always found above the tidal line, but it is possible that environmental factors may play a role in determining host preferences. Additionally, the three mangrove species have different adaptations to surviving salty conditions; *Avicennia* excretes salt through its leaves, *Laguncularia* concentrates salt in special areas of its leaves, and *Rhizophora* excludes salt at the roots (Tomlinson 1986). These physiological traits appear to affect both the relative susceptibility to foliar infection by pathogenic fungi as well as the relative diversity of endophytic fungi of the three host species (Gilbert *et al.* 2002b). Future studies that incorporate the physiological ecology of both the hosts and the fungi may elucidate whether or not salt also plays a role in the ecology of wood-decay fungi in mangrove forests and why polypore fungi have such strong preferences for particular mangrove hosts.

Theory (May 1991) and empirical evidence (Lindblad 2000, Gilbert *et al.* 2002a) suggest that wood-decay polypore fungi in diverse tropical forests are represented by many rare species and that more common species are nonspecialists because host rarity limits the persistence of specialists. Our study indicates that in tropical mangrove forests, where host diversity is low and abundance of individual host species high, this restriction against host specialization may be relaxed, resulting in a polypore community dominated by a few common host-specialist species. The dynamics of specialization in forests of different diversity must be carefully considered in efforts to evaluate the scope and nature of tropical diversity. Incorporation of more focused information on how different ecological or phylogenetic groups of fungi vary in their degree of specificity for host plants or other substrates may provide increased resolution in our efforts to estimate global fungal diversity.

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LITERATURE CITED

Almeida Filho, M., R. Bueno, and V. L. R. Bononi. 1993. Algumas espécies de fungos basidiomicetos dos manguezais do Estado de São Paulo. Hoehnea 20: 87–92.

Aptroot, A. 1997. Species diversity in tropical rainforest Ascomycetes: lichenized vs. non-lichenized; foliicolous vs. corticolous. Abstr. Bot. 21: 37–44.

Arnold, A. E., Z. Maynard, and G. S. Gilbert. 2001. Fungal endophytes in dicotyledonous Neotropical trees: patterns of abundance and diversity. Mycol. Res. 105: 1502–1507.

———, ———, ———, P. D. Coley, and T. A. Kursar. 2000. Are tropical fungal endophytes hyperdiverse? Ecol. Lett. 3: 267–274.

BADER, P., S. JANSSON, AND B. G. JONSSON. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72: 355–362.

BARLOW, B. A. 1992. Conspectus of the genus *Amyema Tieghem* (Loranthaceae). Blumea 36: 293–381.

BILLS, G. F., AND J. D. POLISHOOK. 1994. Abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. Mycologia 86: 187–198.

CANNON, P. F. 1997a. Strategies for rapid assessment of fungal diversity. Biodiv. Conserv. 6: 669–680.

———. 1997b. Diversity of the Phyllachoraceae with special reference to the tropics. *In* K. D. Hyde (Ed.). Biodiversity of tropical microfungi, pp. 255–278. Hong Kong University Press, Hong Kong.

CARRANZA, J. 1996. Distribution of pore fungi (Aphyllophorales: Basidiomycotina) in the biotic units of Costa Rica. Rev. Biol. Trop. 44(suppl. 4): 103–109.

CRAWFORD, R. H., S. E. CARPENTER, AND M. E. HARMON. 1990. Communities of filamentous fungi and yeast decomposing logs of *Pseudotsuga menziesii*. Mycologia 82: 759–765.

DAVIS, J. H. 1940. The ecology and geologic role of mangroves in Florida. Publication no. 517. Carnegie Institute, Washington, D.C.

DURALL, D. M., AND D. PARKINSON. 1991. Initial fungal community development on decomposing timothy (*Phleum pratense*) litter from a reclaimed coal-mine spoil in Alberta, Canada. Mycol. Res. 95: 14–18.

ESPINOSA-GARCIA, F. J., AND J. H. LANGENHEIM. 1990. The endophytic fungal community in leaves of a coastal redwood population—diversity and spatial patterns. New Phytol. 116: 89–97.

FISHER, P. J., AND O. PETRINI. 1990. A comparative study of fungal endophytes in xylem and bark of *Alnus* species in England and Switzerland. Mycol. Res. 94: 313–319.

FRÖHLICH, J., AND K. D. HYDE. 1999. Biodiversity of palm fungi in the tropics: Are global fungal diversity estimates realistic? Biodiv. Conserv. 8: 977–1004.

GILBERT, G. S., A. FERRER, AND J. CARRANZA. 2002a. Polypore fungal diversity in a moist tropical forest. Biodiv. Conserv. 11: 947–957.

———, M. MEJÍA-CHANG, AND E. ROJAS. 2002b. Fungal diversity and plant disease in mangrove forests: salt excretion as a possible defense mechanism. Oecologia. In press.

GILBERTSON, R. L., AND L. RYVARDEN. 1986. North American polypores, vols. 1 and 2. Fungiflora, Oslo, Norway.

HAWKSWORTH, D. L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycol. Res. 95: 641–655.

HUHNDORF, S. M., AND D. J. LODGE. 1997. Host specificity among wood inhabiting Pyrenomycetes (Fungi, Ascomycetes) in a wet tropical forest in Puerto Rico. Trop. Ecol. 38: 307–315.

HYDE, K. D. 1988. Studies on the tropical marine fungi of Brunei. Bot. J. Linn. Soc. 98: 135–151.

———. 1990. A comparison of the intertidal mycota of five mangrove tree species. Asian Marine Biol. 7: 93–107.

——— (ED.). 1997. Biodiversity of tropical microfungi. Hong Kong University Press, Hong Kong.

———, AND E. B. G. JONES. 1988. Marine manglicolous fungi. Marine Ecol. (P.S.Z.N.I.) 9: 15–33.

———, AND S. Y. LEE. 1995. Ecology of mangrove fungi and their role in nutrient cycling: What gaps occur in our knowledge? Hydrobiologia 295: 107–118.

IMBERT, D., AND S. MÉNARD. 1997. Structure de la végétation et production primarie dans la mangrove de la Baie de Fort-de-France, Martinique (F.W.I.). Biotropica 29: 413–426.

JOB, D. J., AND M. RAJCHENBERG. 1988. Experimental wood-rot of *Salix humboldtiana* blocks by species of *Phellinus* Quel. (Aphyllophorales). Mater. Organ. 23: 21–30.

JONES, E. B. G., AND S. A. ALIAS. 1997. Biodiversity of mangrove fungi. *In* K. D. Hyde (Ed.). Biodiversity of tropical microfungi, pp. 71–92. Hong Kong University Press, Hong Kong.

LINDBLAD, I. 2000. Host specificity of some wood-inhabiting fungi in a tropical forest. Mycologia 92: 399–405.

LODGE, D. J. 1997. Factors related to diversity of decomposer fungi in tropical forests. Biodiv. Conserv. 6: 681–688.

MAY, R. M. 1991. A fondness for fungi. Nature 352: 475–476.

MCKEE, K. L. 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. Oecologia 101: 448–460.

NORTON, D. A., AND M. A. CARPENTER. 1998. Mistletoes as parasites: host specificity and speciation. Trends Ecol. Evol. 13: 101–105.

POLISHOOK, J. D., G. F. BILLS, AND D. J. LODGE. 1996. Microfungi from decaying leaves of two rain forest trees in Puerto Rico. J. Ind. Microbiol. Biotechnol. 17: 284–294.

RENVALL, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1–51.

ROSSMAN, A. Y. 1994. A strategy for an all-taxa inventory of fungal biodiversity. *In* C. I. Peng and C. H. Chou (Eds.). Biodiversity and terrestrial ecosystems, pp. 169–194. Institute of Botany, Academia Sinica Monograph Series No. 14, Taipei, Taiwan.

RYVARDEN, L., AND I. JOHANSEN. 1980. A preliminary polypore flora of East Africa. Fungiflora, Oslo, Norway.

SCHAEFFER-NOVELLI, Y., G. CINTRON-MOLERO, R. R. ADAIME, AND T. M. DE CAMARGO. 1990. Variability of mangrove ecosystems along the Brazilian coast. Estuaries 13: 204–218.

SHERMAN, R. E., T. J. FAHEY, AND J. J. BATTLES. 2000. Small-scale disturbance and regeneration dynamics in a Neotropical mangrove forest. J. Ecol. 88: 165–178.

SOTÃO, H. M. P., V. L. R. BONANI, AND T. S. FIGUEIREDO. 1991. Basidiomycetes de manguezais da Ilha de Maracá, Amapá, Brasil. Bol. Mus. Para. Emilio Goeldi Sér. Bot. 7: 109–114.

SOUSA, W. P., AND B. J. MITCHELL. 1999. The effect of seed predators on plant distributions: Is there a general pattern in mangroves? Oikos 86: 55–66.

Tan, T. K., and W. F. Leong. 1992. Lignicolous fungi of tropical mangrove wood. Mycol. Res. 96: 413–414.

Thompson, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago, Illinios.

Tomlinson, P. B. 1986. The botany of mangroves. Cambridge University Press, Cambridge, England.

Wright, J. E., and S. N. Blumenfeld. 1984. New South American species of *Phellinus* (Hymenochaetaceae). Mycotaxon 21: 413–426.

Zhou, D., and K. D. Hyde. 2001. Host-specificity, host-exclusivity, and host-recurrence in saprobic fungi. Mycol. Res. 105: 1449–1457.