



## Polypore fungal diversity and host density in a moist tropical forest

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**Abstract.** In a moist tropical forest in Panama, the wood-decay polypore fungi comprise many rare species (more than half found only once) and exhibit diversity that exceeds that of the supporting tree community. The most abundant fungal species were non-specialists, each found on several host species from multiple plant families. In diverse fungal communities, each of many species should infect a given host species in a density-dependent manner, so that the infected proportion of a host population should increase with host density. Applied across host species, hosts with denser populations should support greater fungal diversity. For 10 tree species, fungal incidence and diversity increased with abundance of the host in the community, consistent with across-species density-dependent infection. Fungal diversity associated with individual trunks did not, however, vary with host-species density. Both host density and persistence of decaying logs may be important in determining fungal diversity associated with tree species.

### Introduction

Moist tropical forests are renowned for their complex layers of biological diversity. One of the best studied neotropical forests, the 1500-ha Barro Colorado Island in Panama, is covered with lowland moist semi-deciduous forest that includes 409 species of trees and shrubs, nearly 200 species of epiphytic flowering plants, 717 known species of homopterans, and more than 300 species of birds (Foster and Hubbell 1990; Karr 1990; Wolda 1996). As has been found in tropical forests around the world, species frequency distributions for many taxonomic groups indicate that a few species are common, but that most species are rare (Price et al. 1995; DeVries et al. 1997; Poulsen and Krabbe 1997; Basset 1999). On a 50-ha plot in old-growth forest on Barro Colorado Island, 49% of the 303 woody plant species (238000 individuals) were represented by fewer than 100 individuals ( $2 \text{ ha}^{-1}$ ), while less than 3% had more than an overall density of more than  $80 \text{ ha}^{-1}$  (Hubbell and Foster 1986). Similarly, of 717 species of homoptera identified from almost 90000 individuals, 168 species (23%) were represented by a single individual and only 9%

of the species were found more than 100 times (Wolda 1996). Despite the recognized megadiversity of tropical fungi (Hawksworth 1991; Arnold et al. 2000), we are largely missing systematic studies of this group, as well as a broader understanding of how the diversity of one group of organisms relates to the density of organisms on which they depend for food.

Polypore fungi hold key roles in forests as pathogens and wood decomposers (Rayner and Boddy 1988; Lisiewska 1992). They are particularly amenable to field study because they produce large, easily seen fruiting bodies that persist for several months to years. In contrast to nearly all other tropical fungi, their taxonomy is relatively well developed (Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1986). Additionally, although their ecological roles range from primary pathogens to saprotrophs (with some species playing multiple roles), they are united in being almost entirely restricted to growth on wood. This restriction also means that they have a well-defined substrate for sampling. Some species exploit numerous host species, whereas many others specialize on one or a few hosts (Farr et al. 1989). Data on host range in the tropics are extremely poor, however, because it is extremely difficult to identify host species, particularly when the fruiting bodies are produced on dead trees or fallen trunks. Recently, Lindblad (2000) found that only 3 of 32 common species of polypore fungi in a Costa Rican dry forest showed any host specificity, but similar studies in moist tropical forests have yet to be undertaken. The 50-ha Forest Dynamics Project (FDP) plot on Barro Colorado Island provides a unique opportunity to systematically study the diversity of polypore fungi and their relationships to host trees in a highly diverse tropical forest. On the FDP plot, all individuals of more than 300 species of free-standing woody plants have been tagged, mapped, identified, and periodically censused since 1981 (Hubbell and Foster 1983; Condit et al. 1994, 1996), providing accurate measures of the relative abundance of tree species. Most importantly, even dead trees retain their identifying tags for years, and exact locations of tagless individuals can be easily measured, so that even decaying trunks of any trees that have died since 1981 can be identified to species.

Here we present the first systematic study of the relationship between the diversity and structure of assemblages of fungi and their plant hosts in a tropical rain forest. We address three issues: the overall structure of the polypore fungal community, the relative frequency of specialist and non-specialist fungi, and the importance of density-dependent infection on structuring the fungal community.

Because most tree species are rare in a diverse tropical forest and thus host availability for specialist fungi is low, we expect the most successful fungi in tropical forests to be non-specialists (May 1991). Common host species should be best able to support specialist fungi, both because the reduced distance to a conspecific tree would increase the chances of successful dispersal of the fungus to a suitable host, and because common tree species may offer a greater range of microclimatic conditions, physiological statuses, and infection courts that ensure that suitable host–fungus environmental combinations are available for successful infection. Such effects of host abundance and suitability would be particularly important if fungi in tropical forests are dispersal limited, as suggested by studies on

distribution of diseases and endophytic fungi in tropical forests (Gilbert et al. 1994; Arnold et al. 2002) and of temperate forest polypores (Moykkynen et al. 1997). Throughout, 'host preference' includes the sum of the genetic, physiological, and ecological conditions associated with particular hosts that confers a preference for certain hosts over others. Overall, we expect to find a fungal assemblage with a few common non-specialists and a large number of rare fungi that may or may not be host specialists.

Finally, we examine the relationship between fungal diversity and density-dependent infection of hosts, where a particular fungus colonizes a greater proportion of a tree population at high host density than at low. Density-dependent colonization of plants by fungi is a nearly universal phenomenon for fungal infection of plants in both natural and managed ecosystems (Burdon and Chilvers 1982; Augspurger and Kelly 1984; Gilbert et al. 1994), but nearly all studies examine the phenomenon in the context of one fungus on one host plant grown at different densities. If instead we consider that each of many fungal associates of a tree species can separately colonize a host population in a density-dependent manner, then we predict that as host population density increases, so would the fungal diversity found on that host.

## Methods

In a transect-based survey on the 50-ha Forest Dynamics Project plot on Barro Colorado Island in Lake Gatun, Republic of Panama, we systematically collected all fruiting bodies (basidiomata) of polypore fungi (families Polyporaceae, Hymenochaetaceae, Ganodermataceae, Corticiaceae) growing on identifiable woody substrates (standing dead, fallen trunks, or live trees) in five north-south transects ( $500 \times 10 \text{ m}^2$ ) spaced 200 m apart on the FDP plot. This method detects only reproducing fungi, and not all vegetative individuals present in the study area. Studies based on fruiting bodies are useful first indicators of polypore diversity in a forest, and have been widely used (Lindblad 2000; Bader et al. 1995), but are likely to underestimate the total diversity of polypores in a site. Collections were all made during the late wet season (November–December) in 1993, when the year's annual basidiomata have already been produced but have not yet decayed (G.S. Gilbert, personal observation). Multiple basidiomata of the same fungal species on a host individual were considered as one fungal collection. Non-poroid polypore allies in the Corticiaceae were not collected in this survey. All collections were determined to species or classified to morphospecies according to standard macroscopic and microscopic characteristics (Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1986) through consultation with appropriate literature and comparison with specimens in the fungal herbarium at the Universidad de Costa Rica. Voucher specimens were deposited at the Herbarium of the University of Panama. The complete species list is available from the senior author upon request. Host species were identified using the FDP database, made available by Condit, Foster, and Hubbell.

To test for evidence of host preferences within this collection, we completely randomized the fungal species across all the collections, maintaining the same

Table 1. Number of trees examined, density of each species on the FDP plot in 1990, estimated half-life of dead trunks, and the incidence and diversity of polypore fungi found in a focal-tree study.

Host tree (code)	Host family	Log (live trees in 1990)	Total no. of trees (% dead)	Half-life of dead trunks (year)	Percentage of live trees with fungi	Percentage of dead trees with fungi	No. of fungi collected (no. of species)
<i>Gustavia superba</i> (Gs)	Lecythidaceae	2.92	92 (6.5)	2.0	3.5	66.7	12 (10)
<i>Pterocarpus rohrii</i> (Po)	Fabaceae	3.23	101 (9.9)	1.8	1.1	50.0	6 (6)
<i>Pouteria reticulata</i> (Pr)	Sapotaceae	3.25	106 (13.2)	11.1	32.6	92.8	52 (13)
<i>Poulsenia armata</i> (Pa)	Moraceae	3.33	108 (13.0)	3.0	1.1	42.9	9 (9)
<i>Quararibea asterolepis</i> (Qa)	Bombacaceae	3.37	109 (17.4)	12.3	3.3	42.1	17 (11)
<i>Protium tenuifolium</i> (Pt)	Bursaraceae	3.49	111 (19.8)	56.3	8.9	54.5	26 (20)
<i>Tachigali versicolor</i> (Tv)	Fabaceae	3.49	110 (16.4)	13.4	2.2	50.0	21 (16)
<i>Tetragastris panamensis</i> (Tp)	Bursaraceae	3.61	112 (18.8)	17.2	0.0	61.9	31 (20)
<i>Alseis blackiana</i> (Ab)	Rubiaceae	3.93	114 (18.4)	20.2	16.1	38.1	29 (22)
<i>Trichilia tuberculata</i> (Tt)	Meliaceae	4.12	84 (39.3)	60.8	3.9	63.9	52 (35)

number of collections per host species as in the original collection. We then tabulated which of the fungal species were found multiple times (and with what frequency) on each host species. This randomization was repeated 999 times (plus the original order) to determine the frequency with which we would expect the observed pattern of apparent host preferences to arise at random.

To calculate the half-life of dead trunks on the forest floor (an estimate of the longevity of the resource in the forest) we used the proportion of trunks found extant in 1994 of those that were alive in 1985 but dead in the 1990 census. We adapted the method described by Sheil et al. (1995), where the exponential mortality coefficient  $\lambda = (\ln(\text{no. of dead in 1990} / \text{no. of trunks extant 1994})) / 6.5$  years, and the half-life  $t_{0.5} = \ln(2) / \lambda$ . We chose a median time of 6.5 years since death because the trees could have been dead for anywhere from 4 to 9 years.

To test the prediction of greater fungal diversity associated with more common host species in a diverse community, we selected 10 tree species with a range of densities on the FDP plot. In this study the same types of fungi were collected as in the general survey, with the inclusion of non-poroid taxa in the Corticeaceae. Host species were selected to ensure a range of densities on the plot and to include species of ecological interest on Barro Colorado Island, but without any regard to wood quality, information about fungal associates, or taxonomic affiliations. With one exception, sampling effort was equal for each host species. We visited 100 individuals selected randomly from the FDP database that were known to be alive in 1990 (only 65 were visited for the most common species, *Trichilia tuberculata*, due to an accounting error). Additionally, we visited 30 of the largest individuals that died between 1985–1990. The final tally of live and dead trees reflects trees that died after 1990, minus trees that were completely decomposed by the 1994 census. Tree species, sample sizes, and species codes are shown in Table 1.

## Results

In the 2.5-ha transect-based fungal survey we found 92 basidiomata representing 43 fungal species; fungi were found on 34 host species from 23 families (66 individuals). Figure 1 shows the cumulative numbers of fungal species and host species encountered as a function of number of fungal collections, in random order. This transect-based study showed that the high tree species diversity supports an even higher diversity of polypore fungi. As is common for many taxa in tropical forests, most fungal species were rare, with 58.1% found only once. As predicted, the most common fungi were host non-specialists; the five most common (4–10 collections per species) each had multiple host species from multiple families. However, it is unlikely that an individual species is able to colonize more than a subset of the many woody species locally available.

We found no evidence for strong host preferences within the collection. Of the 17 species found more than once, eight were found multiple times on a given host species. However, randomization tests of the host–fungus combinations in this collection indicated that this is fewer multiple occurrences than expected at random.

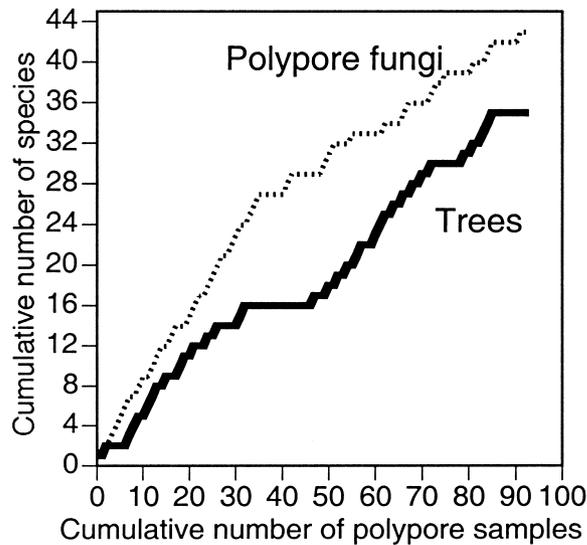
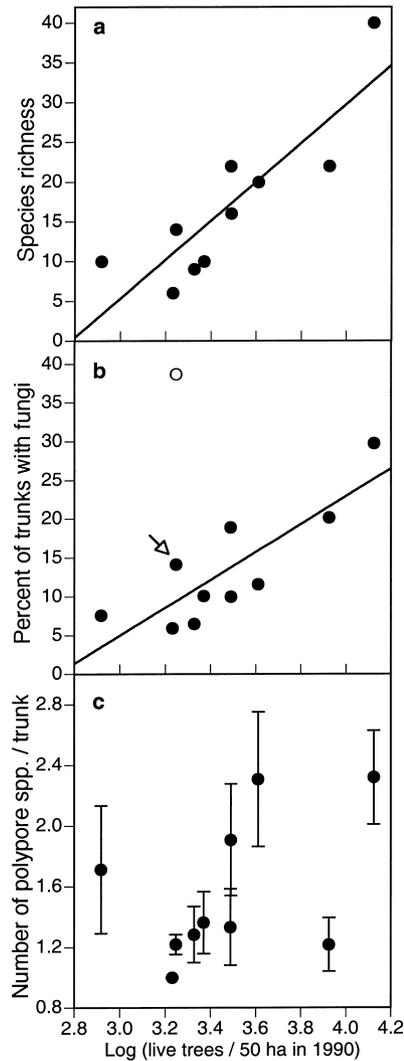


Figure 1. Transect-based study of the diversity of polypore fungi and their host trees found in old-growth lowland tropical forest on Barro Colorado Island, Panama. Shown is the cumulative number of fungal species and host species encountered in 2.5 ha as a function of number of fungal collections.

Furthermore, none of the fungal species were found on fewer host species, or had a higher number of multiple collections on individual host species, than expected at random ( $P > 0.05$  for all comparisons). Thus, we find no evidence for strong host specificity among the more common members of this polypore community.

To test the prediction that greater fungal diversity is associated with more common host species in a diverse community, we selected 10 focal tree species with a range of densities on the FDP plot (Figure 2). With similar sampling intensity across the 10 tree species, we examined 1055 trees, from which we made 257 polypore collections, comprising 110 fungal species. Most of the fungi were found on dead trunks, with a mean of 56% of dead logs having polypore fruiting bodies compared to only 7% on live trees (Table 1). Only *Pouteria reticulata* (with 32.6%) and to a lesser extent *Alseis blackiana* (16.1%) had substantial numbers of fungi associated with live trees. For *Pouteria*, the high incidence of fungi was mostly due to a single corticeaceous species associated with the bark of 24.5% of the trunks; no other fungus was ever found on more than 5.5% of any host species.

Despite equal sampling effort, the number of dead trees encountered in 1994 was strongly correlated with the overall 1990 live density of the species in the plot (no. of dead =  $-50.557 + 19.6807 \log(\text{live } 1990)$ ;  $P \leq 0.0002$ ,  $R^2 = 0.83$ ) (Table 1). This pattern could be the result of either density-dependent mortality (as reported for this site by Wills et al. 1997) or due to greater longevity of dead trees on the forest floor. There was no significant relationship between the density of the host species in 1990 and published mortality rates on the FDP plot for 1982–1985 or 1985–1990 (Condit et al. 1996) ( $P = 0.73$ ,  $R^2 = 0.02$  for 1982–1985;  $P = 0.95$ ,  $R^2 = 0.01$  for



*Figure 2.* Focal-species study on the relationships between the diversity of polypore fungi and host abundance, for 10 tree species on Barro Colorado Island. Tree species, sample sizes, and species codes are as shown in Table 1. (a) Fungal species richness ( $S$ ) vs. the log number of live individuals for each tree species on the entire 50-ha FDP plot in 1990 (Condit et al. 1996) (host abundance) (linear regression  $S = -68.0 + 24.4 \log(\text{live trees})$ ;  $R^2 = 0.74$ ,  $F_{1,8} = 23.2$ ,  $P = 0.001$ ). Host species from left to right (in all three panels), Gs, Po, Pr, Pa, Qa, Pt (upper point), Tv (lower), Tp, Ab, Tt. (b) Percent of trunks with at least one fungal fruiting body vs. host abundance. For Pr (open circle), 24.5% of trunks had a single fungal species associated with the bark; excluding this one extremely unusually common species (no other fungus was ever found on more than 5.5% of host individuals), only 14.2% of trunks of *Pouteria* had fungal associates (closed circle with arrow) (% with fungi =  $-49.0 + 17.97 \log(\text{live trees})$ ;  $R^2 = 0.70$ ,  $F_{1,8} = 18.3$ ,  $P = 0.003$  with closed circle;  $P = 0.24$  with open circle). (c) Mean number of different fungal species per trunk ( $\pm$  standard error) vs. host abundance ( $P = 0.22$ ).

1985–1990), or with the number of newly dead trees in the random sample of trees that were alive in 1990 ( $P=0.34$ ,  $R^2=0.15$ ), arguing against the density-dependent mortality hypothesis. On the other hand, the dead trunks of common species had a significantly longer half-life ( $t_{0.5}$ ) than did trunks of rare species ( $t_{0.5} = -127.1 + 42.28 \log(\text{live } 1990)$ ;  $P \leq 0.02$ ,  $R^2 = 0.47$ ). These findings imply that common host species are a more ecologically reliable substrate for fungal colonists, both because there are greater numbers of the common species on the plot and because dead and dying trunks (the preferred substrate for polypore reproduction) persist longer in the environment. Throughout we will use live density in 1990 as a measure of the commonness of the host, recognizing that it reflects both density and persistence.

Despite the lack of evidence for strong host preferences in the transect surveys, there was a strong positive relationship between the fungal diversity on a host species and the density of that host (Figure 2a). This increase in diversity is apparently a direct effect of density-dependent infection of host populations by many species of polypore fungi (Figure 2b), which suggests some degree of local host preference. Additionally, the presence of density-dependent infection by the polypore assemblage suggests dispersal limitation for fungi in the forest, which would most severely affect fungi with preferences for locally rare hosts. There is no indication that individual trunks of common hosts support a greater diversity of fungi than do individual trunks of rare species (Figure 2c). These relationships between fungal diversity or abundance and host density are not spurious effects of different sampling successes for the different host species, because there were no significant correlations between the number of individuals of each host species visited and fungal species richness ( $R^2 = 0.087$ ), percent of trunks with fungi ( $R^2 = 0.10$ ), or number of fungal species per trunk ( $R^2 = 0.136$ ). Indeed, the most diverse fungal assemblage was associated with *T. tuberculata*, for which the smallest number of logs was visited.

## Discussion

Even a restricted look at a small group of substrate-specialized fungi like the wood-decay polypores demonstrates the tremendous diversity of fungi present in moist tropical forests. As is the case for many tropical taxa, most polypore species on Barro Colorado Island were rare (58% found only once), comparable to leaf-endophyte fungi at this same site (59% singletons; Arnold et al. 2000) and somewhat greater than for polypore fungi in a dry tropical forest in Costa Rica (36% singletons; Lindblad 2000).

Common fungi were all characterized by broad host ranges, as would be expected if dispersal to a suitable new substrate were limited (i.e., because fungal dispersal abilities are less than those required to reach new, rare, susceptible hosts). Host specificity of polypore fungi ranges from extreme generalist to very specific (Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1986; Farr et al. 1989),

although there are very few data for hosts among most collections of tropical polypores. Lindblad (2000) also found little host specialization among tropical polypores, reporting that only 9.4% of common dry-forest taxa showed some degree of specialization. This may be a liberal estimate of specificity, as two of those three species were actually found on hosts from multiple families. Lack of statistical evidence for an excess of host-specific fungi does not exclude the existence of specialists, however. In the present study, for instance, *Phellinus apiahynus* was found multiple times, exclusively on live, but hollow *Ocotea whitei* (Lauraceae); its previous description from *Ocotea* spp. in South America and Africa (Renvall and Niemela 1993) suggests that this may be a host-specialized pathogenic fungus. Similarly, we cannot statistically assess the specificity of the singleton taxa that make up the majority of the polypores collected, although host-specialized fungi are more likely to be rare in the diverse forest and many of the singletons may be specialists.

Specificity among other groups of fungi may be higher, similar to patterns found for insect herbivores on Barro Colorado Island, where 85% of 46 herbivore species were specialized to plants within the family level, with 26% specialized on a single plant species (Barone 1998). In a recent study of leaf-inhabiting fungi from two host plant species on Barro Colorado Island, Arnold et al. (2000) found 62% of 76 non-singleton fungal taxa restricted to one of two hosts.

Polypore species richness will be determined both by initial establishment of a species in the forest and subsequent spread and persistence. Among fungi with host preferences, newly immigrating fungi with preferences for locally common hosts would be more likely than rare-host specialists to find a suitable host. Furthermore, once those fungi reproduce they would be more likely to spread to a similar host. The observed pattern of greater diversity of fungi on more common hosts supports the idea of multiple-species density-dependent infection, suggesting some degree of host preference within the local community. Fundamental to further advances in understanding host–fungal diversity relationships in complex natural ecosystems are two important elements. First, determination of variation in dispersal distances for fungi in tropical forests, in order to directly assess the importance of dispersal limitation. And second, an enhanced understanding of the extent of host specificity, and whether specificity occurs at the specific, general, familial, or some other level.

There is no indication that individual trunks of common hosts support a greater diversity of fungi than do individual trunks of rare species. This contrasts with findings from a low-diversity, managed forest in Scandinavia, where dead logs of Norway spruce at high densities supported greater diversities of fungi per log than did logs at low densities (Bader et al. 1995). The relatively constant level of within-log diversity in the present study may reflect competition among fungal species within individual logs, as demonstrated in other systems (Boddy 2000).

On Barro Colorado Island, polypore fungi collectively infected tree species in a density-dependent manner across host species, resulting in common hosts having a proportionally greater number of individuals infected by mostly rare fungal species. As a consequence, the diversity of polypore fungi associated with a tree species increased with the density of the host in the forest. These results suggest that

density-dependent infection by a suite of fungi is strong enough to overshadow other differences in susceptibility to fungal attack among host species. Therefore, the diversity of plant-dependent fungi in tropical forests might not be a simple function of the species richness of available host plants or of particular species composition, but rather the community structure itself may play a dominant role. Additionally, the fungi themselves may also help shape the plant community. Only a portion of the fungi in this study were likely to be primary pathogens; however, when a greater number of fungal species establishes within the population of a common host, it follows that a dense host population may be more likely to eventually harbor a virulent pathogen within its fungal assemblage. The density dependence in colonization of the hosts is consistent with the analysis of tree mortality patterns on the FDP plot (Wills et al. 1997), which suggests that density-dependent mortality may be important in determining the population dynamics of two-thirds or more of the most common tree species.

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