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## Host and habitat preferences of polypore fungi in Micronesian tropical flooded forests

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### ABSTRACT

The distribution and ecological impacts of plant-associated fungi is determined in large part by their degree of specificity for particular host species or environmental conditions. Here we evaluate the host and habitat preferences among the *Aphyllphorales*, a guild of wood-decay basidiomycete fungi usually considered to be host generalists. We determined the patterns of host association in three well-defined, floristically distinct, tropical wetlands — freshwater forested wetlands, saltwater mangrove forests, and peatlands with scattered trees — on the islands of Kosrae and Pohnpei in the Federated States of Micronesia. Of 33 fungal species, 20 were locally rare. Of the 11 species sufficiently common to evaluate habitat specificity, nine showed significant habitat preferences. Of eight species common enough to evaluate within-habitat host specificity, six showed strong host preferences. All except one of the nine habitat-specialized fungi showed either statistically significant host specificity or strong numerical biases toward single host species. Our results suggest that host preferences may be important in shaping the assemblages of wood-decay fungi, and that the effect of environment on the distribution of susceptible plant species, rather than on the fungi themselves, may ultimately drive the apparent habitat specificity of many fungi.

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### Introduction

The natural distribution of plant-associated fungi across broad geographic ranges is determined by a combination of the distributions of suitable hosts and environmental conditions (Brandle & Brandl 2006; Gilbert *et al.* 2007; Jumpponen *et al.* 2004; Lindblad 2000, 2001; Lodge 1997; Ortega & Navarro 2004; Robertson *et al.* 2006; Sarma & Hyde 2001). Many fungi that depend on plants for nutrition (phytophages) are associated with a broad diversity of plant hosts and habitats (Farr *et al.* 2007: <http://nt.ars-grin.gov/fungaldatabases/>). However, phytophages that appear to be generalists globally may be

host specialists within given ecological contexts (Fox & Morrow 1981; Thompson 1982). For example, more than half of the polypore fungi described as pine or spruce specialists in Scandinavia show broad host ranges in China (Dai & Penttila 2006). As a result, using compiled lists of known hosts (e.g. Farr *et al.* 2007: <http://nt.ars-grin.gov/fungaldatabases/>) to infer that phytophagous fungi are host generalists may obscure ecologically important host preferences at the local level. Understanding local host selectivity is important because it affects patterns of spread, density-dependent population dynamics, and in turn the maintenance of biological diversity and aspects of ecosystem function (reviews in Gilbert 2002,

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2005). In addition, fungi that appear to be specific to habitats with particular environmental conditions (e.g. moisture, irradiation, temperature, salinity) may actually be responding to environmentally determined distributions of susceptible host species. Here we examine host and habitat specificity of wood-decay polypore fungi — obligate phytophages generally regarded as having low host specificity — to evaluate the strength of ecological specialization in determining the distribution of fungi in low-diversity tropical forest ecosystems.

Wood-decay polypore fungi (*Aphyllphorales*, basidiomycete fungi from the *Polyporales*, *Hymenochaetales*, and *Gleophyllales*) comprise a well-defined and well-studied guild of obligate phytophages (Gilbertson & Ryvarden 1986; Ryvarden & Johansen 1980). They are often considered to have broad host ranges, with host preferences at broad phylogenetic levels such as conifers versus angiosperms (Chang 1995; Gilbertson & Ryvarden 1986; Lindblad 2000). They consume dead or sometimes living wood and produce relatively persistent, showy reproductive bodies that have made them useful for a number of studies of fungal diversity and specificity in tropical forest ecosystems (Ferrer & Gilbert 2003; Gilbert *et al.* 2002; Lindblad 2000; Lodge 1997; Schmit 2005). In species-rich tropical forests, most polypore fungal species are rare, and there is little evidence for host specificity even among more common species (Gilbert *et al.* 2002; Lindblad 2000; Lodge 1997). In contrast, in a study of polypore fungi in low diversity neotropical mangrove forest, just three polypore species comprised 88 % of all collections, and each of the five species encountered multiple times showed very strong host preferences (Gilbert & Sousa 2002). Preferences among habitat types may be more important than host specificity in determining the distribution of polypore fungi (Lindblad 2001), just as the local environment is a dominant driver in distribution patterns for other groups of phytophagous forest fungi (Gilbert *et al.* 2007; Unterseher & Tal 2006). However, when plant species composition changes across habitats, it becomes difficult to disentangle the relative contributions of host availability and environment toward fungal distributions.

Most tropical forests are recognized for their high diversity of tree species — commonly hundreds of species in 50 ha (Condit *et al.* 2000). Assessing host specificity can be very difficult in such high-diversity settings, where the low density of individual host species means there is little statistical power. Tropical forested wetlands are unusual among tropical forests for their generally low species richness. Neotropical mangrove forests have as few as three or four species; up to a dozen or so may be found in southeast Asian mangrove forests (Ellison *et al.* 1999). Mangrove trees can thrive in saline coastal areas where most other species cannot. Depending on the local topography and tidal conditions, mangrove forests may occupy a thin stretch of coastline or extend further inland, but are flooded often enough with salt water that plants need robust mechanisms to deal with high salinity (e.g. exclusion, excretion, or sequestration of salt) (Tomlinson 1986). Diversity of tropical freshwater wetlands is also often low, probably related to alternating stresses of hypoxia and drought (Lopez & Kursar 2003). In contrast to high-diversity tropical forests, the low natural diversity (and corresponding high density) of tree species in these wetlands allows robust testing of host specificity of phytophagous fungi. At the same time, the

discrete boundaries and contrasting environmental conditions of freshwater and saltwater wetlands allow comparisons of fungal distributions across habitats.

Here we examine the assemblages of wood-decay polypore fungal assemblages associated with saltwater and freshwater wetlands on the islands of Kosrae and Pohnpei; two of the Federated States of Micronesia, to investigate (1) whether polypore fungi show significant habitat biases between freshwater and saltwater wetland habitats within an island; (2) to what degree the fungi are host specialists within a particular habitat; and (3) whether apparent habitat specificity can be explained through host specificity.

## Methods

### Site descriptions

Wood-decay polypore fungi were collected from three habitats: mangrove forests, freshwater forested wetlands, and a peatland with scattered screwpines. Each habitat is characterized by a low number of woody species, with a diversity of families represented in two of them.

In Micronesia, 11 % of all land area that has been inventoried is composed of mangrove habitat, with ten mangrove species present on the islands of Kosrae (5° 16'N, 162°56'; 7 sites) and Pohnpei (6°49'N, 158° 117'E; 7 sites) (Cole *et al.* 1999; Ewel *et al.* 2003). These species are, in order of importance value on Kosrae: *Bruguiera gymnorhiza* (*Rhizophoraceae*), *Sonneratia alba* (*Sonneratiaceae*), *Rhizophora apiculata* (*Rhizophoraceae*), *Nypa fruticans* (*Arecaceae*), *Xylocarpus granatum* (*Meliaceae*), *Lumnitzera littorea* (*Combretaceae*), *Rhizophora stylosa* (*Rhizophoraceae*), and *Rhizophora mucronata* (*Rhizophoraceae*).

On Kosrae, just inland from the mangrove forests, and separated from salt water flooding by slightly higher elevation, are densely forested freshwater wetlands dominated by *Terminalia carolinensis* (*Combretaceae*). This landscape pattern may have once been characteristic of Pohnpei as well (e.g. Hosokawa 1952), but most *Terminalia* trees in Pohnpei have been harvested, and many coastal freshwater wetlands are now dominated by *Hibiscus tiliaceus* (*Malvaceae*). Other woody species, such as *Metroxylon amicarum* (*Arecaceae*), are common in freshwater forested wetlands, as well as a handful of species more commonly found in uplands (MacLean *et al.* 1988). On Pohnpei, a brackish peatland at Nan Panilap is adjacent to mangrove forest and may once have been a stand of mangroves itself (Chimner 2004), but now has only scattered individuals of a single woody species, the screwpine *Pandanus cominsii* (*Pandanaceae*).

There is little overlap in tree species among these wetlands. Mangrove associates *Barringtonia racemosa* (*Lecythidaceae*) and *Heritiera littoralis* (*Sterculiaceae*) may be found in both mangrove forests and freshwater forested wetlands, and *Pandanus cominsii* may be found in some freshwater forested wetlands on Pohnpei as well as in the peatland.

### Collection strategy

Collections of polypore fungi were made from Kosrae and Pohnpei in February 2001. The collection efforts at each site

lasted from 0.5–2.5 h, with one to five people collecting all polypore fungi encountered as they walked haphazardly through each site. Multiple fruiting bodies of the same species, when found on an individual host, were counted as only one collection. Trunks of even decaying logs could be identified to species by local forestry experts, because of the low diversity of trees and their distinctive features. We collected from mangrove forest on Kosrae at Finkol, Utwa, and Yela, and on Pohnpei at Sapwalap and Enipos. We collected from freshwater forested wetlands at Yela on Kosrae and from Alokabw and Pohnlangas on Pohnpei. We also collected from peatland with scattered screwpines at Nan Panilap on Pohnpei.

Fungi were dried and identified based on macroscopic and microscopic morphological characteristics through comparison with appropriate literature and herbarium specimens. Vouchers are deposited in the herbarium of the University of California, Berkeley, USA, and at the University of Oslo, Norway.

### Analyses

We used the Binomial Distribution and Binomial Probability functions of JMP v. 6.0 (SAS Institute, Cary, NC) to calculate the probability that each fungus would be found on a particular host or habitat at the observed frequency or less, or the observed frequency or more, given the relative abundance of that host or habitat in the overall collections. Different sites within a habitat type on a given island were combined for analysis.

We examined host and habitat specificity at several levels, as follows. For each island we tested for differences in fungal distribution across habitats (Kosrae and Pohnpei: mangrove versus freshwater forested wetlands; Pohnpei only: mangrove and freshwater forested wetlands, and screwpine peatland). This test ignores differences in host availability across habitats, so we then tested for host preferences among tree species within mangrove and freshwater forested wetlands, testing independently for each island and habitat. Subsequently, we repeated the testing using only those three host species found commonly in mangrove forests on both islands, with data from mangrove swamps combined across islands. We then tested for differences across islands, within mangrove habitats.

## Results

We identified 33 species among the 173 collections of polypore fungi from forested wetlands in Kosrae and Pohnpei (Tables 1 and 2). Twenty-two species were too rare (usually three or fewer collections) to provide sufficient statistical power to assess their habitat or host specificity. Among the remaining species, we found strong evidence for both habitat and host preferences among the wood-decay polypore fungi.

### Habitat specificity within islands

We found significant habitat preferences for nine of the 11 fungal species (82 %) that were sufficiently abundant for statistical testing (Table 3). Three species (*Phellinus fastuosus*, *Aurificaria luteoumbrina*, and *Coriopsis sanguinaria*) were

strongly associated with mangrove habitat, four species with freshwater forested wetlands (*Microporus affinis*, *Rigidoporus microporus*, *Earliella scabrosa*, and *Ganoderma resinaceum*), and two species were found exclusively in the screwpine peatland (*Trametes lactinea* and *Pycnoporus sanguineus*). In all cases where independent tests were possible for the same fungal species on both islands, the results were consistent.

### Host specificity

Within mangrove habitats, we found significant host preferences for all five of the fungal species that were sufficiently common for statistical testing (Table 1). *Phellinus fastuosus* and *Aurificaria luteoumbrina* were both much more common on *Sonneratia alba* (and much less common on *Rhizophora apiculata*) than expected by chance. *Coriopsis sanguinaria* and *Fomitopsis nivosa* were more common on *Rhizophora apiculata* than expected. Patterns were similar in both islands, although the host preferences were not always significant on Pohnpei. When data from the two islands were combined for the three most common mangrove species (*B. gymnorhiza*, *R. apiculata*, *S. alba*), these patterns were always significant (*P*-values ranged from 0.0001 to 0.0187). Although *Trametes cingulata* was found on three host species in Kosrae, it was disproportionately common on *Bruguiera gymnorhiza*.

In general, the power was too low for statistical tests of host specificity within freshwater habitats, but six of the eight fungi that were collected multiple times were found exclusively or nearly so on single host species, including all but one of the fungi identified as strongly associated with freshwater wetlands.

### Differences between islands

Comparison of the fungi found in mangrove habitats between the two islands showed few strong differences; only *Coriopsis sanguinaria* and *Trametes cingulata* differed significantly (*P* = 0.02) between the islands, although both were present on both islands. *C. sanguinaria* was found exclusively on *Rhizophora apiculata*, whereas *T. cingulata* had one of the broadest observed host ranges. Host composition in freshwater forested wetlands was non-overlapping between the two islands, so direct comparison of the fungi would not be informative.

## Discussion

We found strong indications of host specificity among the polypore fungi collected from forested wetlands in Micronesia. The high levels of host specificity found among fungi collected from mangrove forests (81 % of all collections were from the five species showing significant host preferences) were similar to that found in a mangrove forest in Panama (88 % of collections were host specialized species) (Gilbert & Sousa 2002). This contrasts sharply with very low levels of host specificity in high-diversity tropical forests (Ferrer & Gilbert 2003; Gilbert et al. 2002; Lindblad 2000; Lodge 1997). Such patterns of specificity agree with the prediction that fungi in high-diversity tropical forests should demonstrate low levels of host specificity because of limitations of dispersal among rare hosts

**Table 1 – Wood-decay basidiomycete polypore fungi collected from mangrove forests on the islands of Kosrae and Pohnpei, Micronesia**

Fungus	Kosrae hosts					Pohnpei hosts						Total	
	<i>Bruguiera gymnorrhiza</i>	<i>Rhizophora apiculata</i>	<i>Sonneratia alba</i>	<i>Xylocarpus granatum</i>	P	<i>Bruguiera gymnorrhiza</i>	<i>Heritiera littoralis</i>	<i>Lumnitzera littorea</i>	<i>Rhizophora apiculata</i>	<i>Sonneratia alba</i>	<i>Xylocarpus granatum</i>		P
<i>Phellinus fastuosus</i>	1		<b>15</b>		0.0003 <sup>a</sup>	5		3		14	3	0.1147 <sup>a</sup>	41
<i>Aurificaria luteoumbrina</i>	1		<b>8</b>		0.0224 <sup>b</sup>	1		3		4	2	0.0795	19
<i>Coriopsis sanguinaria</i>		<b>9</b>			0.0001 <sup>c</sup>				<b>2</b>			0.0151	11
<i>Fomitopsis nivosa</i>		<b>5</b>			0.0344	1			<b>2</b>			0.0415	8
<i>Trametes cingulata</i>	3	2	2		0.0395					1		-	8
<i>Rigidoporus vinctus</i>		2			-				1	1		-	4
<i>P. mangrovicus</i>					-						3	-	3
<i>Ganoderma tornatum</i> <sup>d</sup>					-				2			-	2
<i>Tinctoporellus epimiltinus</i>			1		-	1						-	2
<i>Daedalea flavida</i> <sup>e</sup>	1				-							-	1
<i>Diplomitoporus cf stramineus</i>				1	-							-	1
<i>Erythromyces crocicreas</i>					-						1	-	1
<i>Nigrofomes melanoporus</i>					-	1						-	1
<i>Perenniporia tenuis</i>					-					1		-	1
<i>P. tephropora</i>					-					1		-	1
<i>P. caryophylli</i>					-		1					-	1
<i>P. merrillii</i>					-						1	-	1
<i>Rigidoporus microporus</i>					-					1		-	1
<i>Schizopora flavipora</i>					-					1		-	1
Total fungi collected on host	6	18	26	1		9	1	6	7	24	10		108

P-values are for within island tests and indicate the binomial probabilities of finding that many or more occurrences on that host, given the relative frequency of all fungal collections across mangrove hosts on that island. Emboldened values indicate that a species is significantly more common on that host than expected. P-values are shown for all fungi that were sufficiently abundant to allow statistical detection of host preferences; (-) indicates that there was not enough power for that particular test.

a The probability that *Rhizophora apiculata* had no *Phellinus fastuosus* was 0.0009 on Kosrae and 0.03779 on Pohnpei.

b The probability that *Rhizophora apiculata* had no *Aurificaria luteoumbrina* was 0.0199.

c The probability that *Sonneratia alba* had no *Coriopsis sanguinaria* was 0.0016.

d Synonym of *Ganoderma australe*.

e Synonym of *Lenzites acuta*.

**Table 2 – Fungi collected from freshwater forested wetlands on the islands of Kosrae and Pohnpei, Micronesia**

Fungus	Kosrae						Pohnpei				Total
	Terminalia forest						Hibiscus forest			Peatland	
	Areca cathecu	Barringtonia racemosa	Horsfieldia nunu	Neubergia celebica	Terminalia carolinensis	P	Cocos nucifera	Hibiscus tiliaceus	P <sup>a</sup>	Pandanus cominsii	
<i>Microporus affinis</i>		1		1	10	0.09			–		12
<i>Rigidoporus microporus</i>	1	2	2		1	0.21		5	–		11
<i>Earliella scabrosa</i>				1		–		7	–		8
<i>Trametes lactinea</i>						–				6	6
<i>Ganoderma resinaceum</i>						–	<b>4</b>		0.001		4
<i>G. tornatum</i> <sup>b</sup>	1				1	–		2	–		4
<i>Pycnoporus sanguineus</i>						–			–	4	4
<i>Polyporus gramocephalus</i>						–		3	–		3
<i>Antrodiella</i> sp.					1	–			–		1
<i>Ganoderma lucidum</i> s. lat					1	–			–		1
<i>Nigroporus vinosus</i>					1	–			–		1
<i>Phellinus fastuosus</i>		1				–			–		1
<i>P. membranaceus</i>						–		1	–		1
<i>Podocypha nitidula</i>						–		1	–		1
<i>Rigidoporus vinctus</i>					1	–			–		1
<i>Schizophyllum commune</i>			1			–			–		1
<i>Tinctoporellus epimiltinus</i>						–		1	–		1
<i>Trametes cingulata</i>					1	–			–		1
<i>T. menziesii</i>						–	1		–		1
<i>T. pocas</i>						–		1	–		1
Total fungi collected on host	2	4	3	2	17		5	21		10	64

P-values are for within island tests within the freshwater wetland habitat, and indicate the binomial probabilities of finding that many or more occurrences on that host, given the relative frequency of all fungal collections across hosts in the forest on that island. Emboldened values indicate that a species is significantly more common on that host than expected. P-values are shown for all fungi that were sufficiently abundant to allow statistical detection of host preferences; (–) indicates insufficient power for that particular test.

a In a Pohnpei freshwater wetland, 14 collections exclusively on *Hibiscus tiliaceus* would be the minimum required to detect a significant bias for that host.

b Synonym of *Ganoderma australe*.

**Table 3 – Fungi that were sufficiently abundant to allow statistical detection of habitat preferences if a preference indeed existed**

Identification	Kosrae			Pohnpei					KvsP P
	Mangrove	Freshwater	P	Mangrove	Freshwater	P	Peatland	P	
<i>Phellinus fastuosus</i>	16	1	0.0051	25	0	0.0001	0	–	0.186
<i>Aurificaria luteoumbrina</i>	9	0	0.0174	10	0	0.0233	0	–	0.596
<i>Microporus affinis</i>	0	12	0.0001	0	0	–	0	–	–
<i>Rigidoporus microporus</i>	0	6	0.0023	1	5	0.0134	0	–	–
<i>Coriolopsis sanguinaria</i>	9	0	0.0174	2	0	–	0	–	0.021
<i>Trametes cingulata</i>	7	1	0.1514	1	0	–	0	–	0.025
<i>Earliella scabrosa</i>	0	1	–	0	7	0.0003	0	–	–
<i>Ganoderma tornatum</i>	0	2	–	2	2	0.3717	0	–	–
<i>Trametes lactinea</i>	0	0	–	0	0	–	6	0.0001	–
<i>Ganoderma resinaceum</i>	0	0	–	0	4	0.0096	0	–	–
<i>Pycnoporus sanguineus</i>	0	0	–	0	0	–	4	0.0001	–
Total fungi collected	51	29		57	26		10		

The symbol (–) indicates that there was not enough power for that particular test. P-values indicate the binomial probabilities of finding that many or more occurrences in that habitat, given the relative frequency of all fungal collections across habitats (see Tables 1 and 2 for overall frequencies). Comparisons are across habitats (Mangrove versus Freshwater, or Mangrove versus Freshwater versus Peatland) within islands. Emboldened values indicate that a species is significantly more common in that habitat than expected. The last column indicates P-values comparing relative frequency of fungi from mangrove habitats between Kosrae and Pohnpei.

(May 1991). In contrast, where diversity is low and density of individual host species high, host specialists may have an ecological advantage (Gilbert 2005). As expected, studies in low-diversity forests in the temperate zone also have shown host specificity among polypore fungi (La Porta et al. 1998; Ortega & Navarro 2004; Robledo et al. 2006).

We also observed very strong patterns of habitat specificity, with only 18 % of the 33 fungal species found in both freshwater and mangrove forests. However, much of the habitat specificity may be due to specificity for particular hosts that in turn have habitat preferences. Of the 11 testable fungal species, nine (81 %) showed habitat preferences, and of those nine, all except *Microporus affinis* also showed either statistically significant within-habitat host preferences or strong numerical biases toward single host species.

The islands of Kosrae and Pohnpei are separated by nearly 600 km of ocean, but the difference in polypore fungi in mangrove habitat was small. All of the taxa we collected have been described elsewhere in the world on multiple hosts outside of flooded forests. However, there was no overlap with fungi collected from mangrove forest in Panama (Gilbert & Sousa 2002).

Our study has three limitations: first, without experimental manipulations we are unable to distinguish between preferences for a particular host or habitat and aversion to others. Second, we collected basidiomata during a short period, so we would have missed ephemeral species. However, because we collected from all the habitats in a short period and most polypores have persistent basidiomata, our comparisons across hosts and habitats should not be affected. Third, we were unable to determine relative densities of all stems of potential host plants, whether or not they had fungi. Using overall relative abundances is the preferred approach for testing host specificity (Gilbert et al. 2007; Gilbert & Sousa 2002), but because we collected all reproductive structures encountered with no regard to host, we were testing against the relative frequencies of host species that supported reproductive polypore fungi, and our results should be robust.

Our results suggest that even for phytophages with broad global host ranges like wood-decay polypore fungi, host preferences within local ecological contexts can be ecologically important and drive apparent preferences for different habitats.

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