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THE PATCHINESS OF EPIFOLIAR FUNGI IN TROPICAL FORESTS: HOST RANGE, HOST ABUNDANCE, AND ENVIRONMENT

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Abstract. Fungal symbioses affect the diversity, dynamics, and spatial patterns of trees in tropical forests. Their ecological importance is partly driven by their inherent patchiness. We used epifoliar fungi, a guild of common, benign, obligate, fungal symbionts of plants, as a model system to evaluate the relative importance of host phylogeny, host relative abundance, and microclimate on the three-dimensional distribution of plant–fungus symbioses. In parallel studies in rainforests in Panama and Australia, most epifoliar fungi were able to colonize several plant lineages but showed significant host preferences within the local plant community. More closely related plant species were not more likely to share fungal symbionts. Instead, fungal species were more likely to be shared by more abundant hosts, which supported a greater number and diversity of fungi. Environmental conditions strongly affected spatial distributions, with sites in the dark understory 2.5- to fourfold more likely to have epifoliar fungi than in the exposed forest canopy. In the understory, fungal incidence increased with canopy openness. Canopy trees supported only a subset of the fungal symbionts found in the understory, suggesting that adult trees are not reservoirs of these fungal symbionts for understory juveniles.

Key words: canopy access cranes; Cleistanthus myrianthus; *epiphyll; phyloecology; plant–fungus symbiosis; Queensland Australia; San Lorenzo Panama; tropical rainforest canopy.*

Special Feature

Introduction

Fungal symbionts play key ecological and evolutionary roles in tropical forests. Ranging from mutualists to pathogens, symbionts affect individual plant performance, population dynamics, community structure, and diversity of plants (reviews in Saikkonen et al. 1998, Gilbert 2002, Allen et al. 2003). Ecological impacts are modulated by the patchiness of many plant–fungus symbioses, and the distribution and impacts of fungi depend on the biotic and abiotic environment of the interaction (Augspurger 1984, Gilbert et al. 1997, Kiers et al. 2000, Arnold and Herre 2003).

Host selectivity of fungal pathogens and mutualists is of central importance for many aspects of the biology of these interactions. For example, the importance of density- or distance-dependent transmission of plant pathogens will depend on the number of locally present hosts that can be infected and the spatial distribution of those hosts (Gilbert 2005). Studies of polypore fungi, leaf endophytes, and mycorrhizae suggest that polyphagy is probably the rule among tropical fungi, but that local host preferences and differential impacts are common (Arnold et al. 2000, 2001, Kiers et al. 2000). Host specificity can be context dependent; fungi with broad host ranges may dominate diverse forests, while low-diversity forests are dominated by specialists (review in Gilbert 2005). Our understanding of host preferences, however, is in its infancy.

Spatial and temporal variation in plant–fungus symbioses in tropical forests can be generated by density- and distance-dependent infection processes as well as by microclimatic variation (Augspurger 1984, Gilbert et al. 1997, Arnold and Herre 2003, Kyllo et al. 2003). However, pathogens and mutualists could also directly affect the distribution or abundance of the hosts themselves; a virulent pathogen might locally eliminate populations of particular host species in precisely the areas where the pathogens have their greatest effects.

In order to decouple the effects of host distribution on fungi from those of fungi on host distribution, we need a model system in which the fungi are neutral commensals. Epifoliar fungi, or fungal epiphylls, comprise a polyphyletic guild of ascomycete fungi that obligately complete their entire life cycle on the surface of living plant leaves. Epifoliar fungi are functionally commensal with their host plants; they do not cause disease and in general plants can photo-compensate for the light lost to epiphyll cover (Anthony et al. 2002; but see Wood et al. 1988 for an exception). The several hundred known species of tropical epifoliar fungi employ one of several nutritional strategies and include superficial saprobes,

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specialists on insect-produced honeydew, and weak parasites that obtain nutrition directly from the host plant (Reynolds and Gilbert 2005 and references within). The epifoliar fungi we have encountered come from diverse clades within the Ascomycetes (Lutzoni et al. 2004), and each lineage is comprised mainly of obligately epifoliar species found primarily on living leaves (Kirk et al. 2001). Epifoliar fungi are readily visible with the naked eye and have persistent structures useful for identification. They are widespread, show some degree of host preferences, and are affected by microclimatic variation (Barr 1987, Gilbert et al. 1997). These traits make epifoliar fungi useful for investigating the distribution of plant–fungal symbioses in tropical forests, without the complication of direct effects of the fungus on the host itself.

Here, we present epifoliar fungi as a novel system with which to ask critical questions about how host phylogeny, host relative abundance, and environmental conditions determine the distribution of tropical plant–fungal symbioses. We used canopy-access cranes in rainforests in Panama and Australia to assess the three-dimensional patterns of distribution of epifoliar fungi and to evaluate four underlying assumptions of many studies of plant–symbiont interactions in tropical forests: (1) obligate fungal symbionts (and other phytophages) in diverse tropical forests should be polyphagous (May 1991, Novotny et al. 2002), but their host range should be concentrated among closely related hosts (Webb et al. 2006); (2) hosts should be more likely to share fungi with common plant species than with rare ones; (3) environmental conditions shape the distribution and impacts of plant–fungal symbioses (Gillett 1962, Givnish 1999); and (4) adult trees are reservoirs for symbionts that infect nearby offspring (Janzen 1970, Connell 1971).

Methods

We investigated the epifoliar fungi in tropical rainforests in Australia and Panama, using canopy-access construction cranes to access foliage from the top of the canopy to ground level. At each site we collected epifoliar fungi early in the rainy season (1) using radial transects to explore relative abundances and host ranges and (2) from a focal tree species in the canopy and understory to evaluate the likelihood that canopy trees act as fungal reservoirs for understory juveniles.

Site descriptions

The Australian Canopy Crane Research Facility (Stork and Cermak 2003), managed by the Rainforest Cooperative Research Centre, is located in lowland tropical rainforest at Cape Tribulation, near the Daintree National Park, North Queensland, Australia (16°04′ S, 145°28′ E; altitude 40 m). The vegetation is complex mesophyll vine forest with an irregular, storm-damaged canopy from 15 to 33 m tall. The site averages 3600 mm rain annually, with 70% usually falling between December and April. A construction tower crane (Liebherr 91EC; Liebherr International AG, Bulle Switzerland), 47 m tall, with a radius of 55 m, provides full three-dimensional access to about 1.0 ha.

The San Lorenzo Canopy Crane, managed by the Smithsonian Tropical Research Institute, is located in lowland tropical rainforest on the San Lorenzo Protected Area on the Caribbean coast of the Republic of Panama (9°17′ N, 79°58′ W; altitude 130 m; Wright et al. 2003). The vegetation is tropical wet evergreen forest, with a canopy height of 35–45 m. The site averages 3152 mm rain annually. A Krøll K-700 crane (Kr II Cranes A/S, Nordkranvej, Denmark) has a 53-m reach that provides access to 0.9 ha of forest.

Radial-transect surveys for host range and relative abundance

We conducted systematic radial transects along the length of the crane reach, taking samples every 5 m, by collecting three leaves from all plant species within a 2-m radius. Leaves were not inspected for presence of fungi before collection. Parallel transects were run at the top of the canopy and at ground level directly below, providing estimates of the relative abundance of epifoliar fungi and their plant hosts and the ability to analyze both host range and spatial patterns of fungal incidence. At Cape Tribulation, we evaluated microclimate variation by estimating canopy openness using hemispherical digital images at each sample point in the canopy and understory (Appendix A). Fungi were identified based on morphological characters (methods and species list in Appendix B; Reynolds and Gilbert 2005, 2006).

We tested for host selectivity by calculating the probability that epifoliar fungi would never be found on a host species of a given relative frequency, assuming a binomial distribution under the null assumption that epifoliar fungi are host nonselective (Appendix C).

We used logistic regression to evaluate how phylogenetic distance and joint relative abundance (JRA) of hosts affected the probability that pairs of plant species would share taxa of epifoliar fungi. For all identifiable angiosperm plant species sampled in the radial transects, we used the Phylomatic component of Phylocom v3.34 (with the Phylomatic tree R20050610) to produce a tree topology based on the APG II backbone (Angiosperm Phylogeny Group 2003), and branch lengths set using Phylocom bladj function with ages from Wikstrom et al. (2001) (Phylocom v3.34 *available online*).[6] We then used the Phylocom phydist function to create a matrix of pairwise phylogenetic distances (in My) between each pair of plant taxa. We excluded samples from non-angiosperm hosts and samples for which the host could not be identified reliably at least to the family level. For each pair of plant species we calculated the joint relative

[6] ⟨http://www.phylodiversity.net/phylocom⟩

TABLE 1. Epifoliar fungi collected in radial transects in the canopy and understory of the rain forest at San Lorenzo, Panama, and Cape Tribulation, Australia.

Stratum	No. sample sites (% with fungi)	No. plant samples (% with fungi)	No. plant species (% with fungi)	No. fungal collections	No. fungal species
Panama					
Canopy	72 (43.0%)	75 (16.1%)	31 (29.0%)	17	8
Understory	72 (16.7%)	489 (8.2%)	148 (18.24%)	54	21
Total	144 (29.9%)	564 (9.2%)	166 (20.5%)	71	23
Australia					
Canopy	120 (35.8%)	255 (4.3%)	68 (10.3%)	14	10
Understory	120 (9.2%)	588 (11.6%)	129 (27.1%)	95	24
Total	240 (22.5%)	843 (9.4%)	167 (23.9%)	109	25

abundance as the product of the proportion of all plant samples for those species (e.g., two species of 2% relative abundance each have a joint relative abundance $= 0.02 \times 0.02 = 0.0004$). We then used Proc Logistic (SAS, version 8.0; SAS Institute 2001) to select the best of all possible models using the independent variables phylogenetic distance, joint relative abundance (or $\log_{10}$[JRA]), and the interaction (Appendix D).

Focal host survey: canopy–understory connection

Cleistanthus myrianthus (Euphorbiaceae) is common in the Australian plot and was frequently colonized by epifoliar fungi both as mature canopy trees and as understory juveniles. We randomly selected 24 of the 73 mapped mature trees and determined whether they harbored epifoliar fungi by carefully examining (2 min with a hand lens) all reachable foliage (~2 m radius), at each of three different haphazardly chosen positions and levels of the tree crown. For all conspecific juveniles within 3 m of the trunk base (juvenile density), we inspected all leaves to determine if they were colonized by epifoliar fungi (20 adults and 50 juveniles total). Fungi collected from both the adults and juveniles were identified. Canopy openness at a point 1 m south of each canopy tree was estimated from the mean of four readings from a spherical densiometer taken at cardinal directions (1.3 m above the ground). We used logistic regression to test whether canopy openness, juvenile density, or the colonization status of the nearest canopy tree affected whether a juvenile was colonized by epifoliar fungi (Appendix E).

RESULTS

Abundance and diversity of fungi and their hosts

In the radial transects, epifoliar fungi were found on about 9% of the plant samples at each site (Table 1). This included 23 of 28 epifoliar species (Panama) and 25 of 35 species (Australia) found during extensive collections at the two sites (Reynolds and Gilbert 2005, 2006; D. R. Reynolds, G. S. Gilbert, and A. Bethancourt, *personal observation*), indicating a reasonably thorough fungal sampling (Appendix B).

Epifoliar fungi showed preferences among locally available plant species, being absent from 79.5% (Panama) and 76.1% (Australia) of all sampled plant species. Accounting for the rarity of hosts, this proportion was much higher than expected by chance if fungi had no host selectivity (Appendix C). For instance, in Panama, plant species of frequency 1, 2, 3, 4, or 5 in the collection (89% of all plant species at the site) were more often fungus-free than would be expected by chance ($P = 0.015$, 0.052, 0.039, 0.089, 0.067, respectively). In addition, even some very common hosts were unexpectedly free of epifoliar fungi (Australia, *Merremia peltata* [58 collections; $P = 0.0003$]; Australia, *Calamus radicalis* [28 collections; $P = 0.021$]; Panama, unidentified Fern 1 [23 collections, $P = 0.045$]).

Diversity of epifoliar fungi and their host plants was similar in Panama and Australia (Appendix B). The 23 species of epifoliar fungi in Panama were found on 32 identifiable vascular plant species (plus 4 unidentified), from at least 29 genera, 22 families, and 17 orders. Similarly, the 25 fungal species found in radial transects in Australia were distributed across 40 plants species from at least 27 genera, 19 families, and 17 orders.

Phylogeny and relative abundance in host range determination

Although epifoliar fungi clearly show preferences for some plant species over others, we found no evidence for the expected phylogenetic signal in host range. Epifoliar fungi were polyphagous: all but one fungal species collected three or more times were found on multiple plant orders, and at neither site was the phylogenetic distance between plant species predictive of the probability of sharing fungal symbionts (Appendix D). In contrast, more common plants were much more likely to share fungal species than were rare plants. At both sites, the logarithm of the joint relative abundance of host plants was a strong indicator of the likelihood of sharing fungal symbionts, correctly predicting 63% (Panama) and 71% (Australia) of fungal sharing between plant species (Fig. 1 and Appendix D). Greater sharing may be a function of abundant plants being more likely to

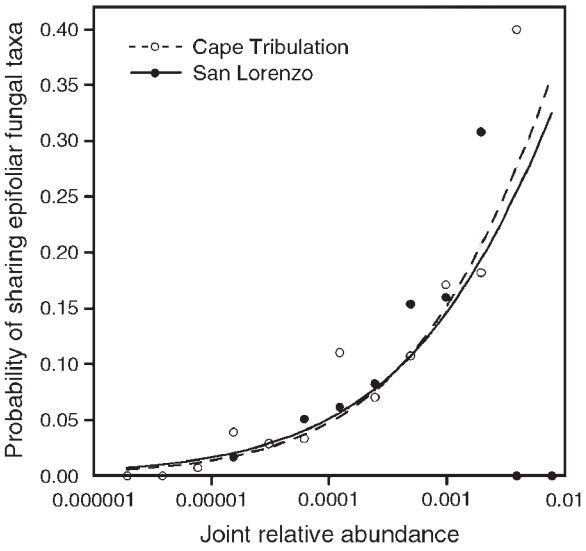

FIG. 1. The probability that two plant species share epifoliar fungal symbionts in the rain forest at Cape Tribulation, Australia, and San Lorenzo, Panama. Points indicate the proportion of host species pairs that shared at least one fungal taxon at that binned joint relative abundance (JRA). Lines are the predicted probabilities from best-fit logistic regression models (Appendix D). For each line, $p(\text{sharing}) = e^y/(1 + e^y)$ where $y = 2.0995 + 1.2722 \log_{10}(\text{JRA})$ for Panama and $y = 1.7059 + 1.1563 \log_{10}(\text{JRA})$ for Australia.

encounter compatible fungi under appropriate conditions.

Canopy–understory distribution of epifoliar fungi

Epifoliar fungi were much more common and diverse at sample sites in the understory than in the canopy (Panama, 43.0% vs. 16.7%, respectively, Fisher's exact test $P = 0.0009$; Australia, 35.8% vs. 9.2%, $P \leq 0.0001$) (Table 1). Similarly, in Australia, the proportion of understory plant samples with fungi was twice that in the canopy. However, in Panama there were many fewer host species in the canopy, and because rare species in the understory tended to be free of fungi, the pattern there was reversed (Table 1). This difference was largely due to the much more dominant presence of climber species and greater plant diversity in the Australian canopy.

All but three of the 18 fungal species found in the canopy (both sites combined) were also recorded in the understory (Appendix B), suggesting that the canopy mycota is a nested subset of that in the understory. The three canopy-only species were each found only once or twice.

In only one case (both sites combined), was the same fungal species found in both the canopy sample point and the understory sample point directly below. This lack of fungal connection between strata may reflect the differences in composition of potential plant hosts in the canopy and understory. Although the forest canopy has a high density of leaves, the plant diversity per sample site was much less than in the understory (Panama, canopy 1.04 ± 0.37 species vs. understory 6.69 ± 2.47 species [mean ± SD], paired $t = 18.25$, df = 71, $P \leq 0.0001$; Australia, canopy 2.14 ± 1.17 vs. understory 4.91 ± 2.07, paired $t = 12.52$, df = 119, $P \leq 0.0001$). Few plant species were shared between canopy and understory (Panama, 10 of 92 species, 10.9%; Australia, 30 of 167 species, 17.9%).

In addition to host distribution, environmental conditions differ between the canopy and understory (Appendix A), and may limit the distribution of different species of fungi to one stratum or the other. To test the effect of microclimate on the patchiness of fungal symbioses and explore the potential of mature trees as fungal reservoirs, we studied fungi associated with a single common host.

Focal host: canopy–understory connection

Cleistanthus myrianthus is an unusually good host for epifoliar fungi, representing 38% of the fungal collections and half of the fungal species recorded from the Australian canopy, with less than 3% of the leaf collections. Fungi were found on 75% of canopy adults and 28% of understory juveniles. Logistic regression indicated that neither juvenile density nor the colonization status of the nearest adult significantly affected the probability of finding epifoliar fungi on a juvenile (Appendix E). However, juveniles in more open environments were much more likely to have epifoliar symbionts. The regression $y = -2.8624 + 0.2729(\text{canopy openness})$, where $p(\text{juvenile colonized}) = e^y/(1 + e^y)$ (AIC = 54.48 , $\chi^2 = 8.82$, $P = 0.003$), correctly predicted which juveniles were colonized by epifoliar fungi 72.6% of the time.

Of the 12 fungal species found on *Cleistanthus myrianthus,* there was little overlap between the adult crown and understory juveniles (Fig. 2). Canopy foliage was more frequently colonized by epifoliar fungi, but species richness was much lower, dominated by *Stomiopeltis gautheriae*, a canopy specialist (Fisher's exact test, $P \leq 0.0001$). In fact, only two fungal species were found in both strata, and neither were on the canopy tree above the understory collections. All species except *Hymeniodiopeltis major* were found on other hosts (Reynolds and Gilbert 2005); the fungi of *C. myrianthus* appear to be stratum specialists rather than host specialists.

DISCUSSION

Epifoliar fungi represent a novel and tractable system for investigating a range of questions about host range, host abundance, and environmental influences on the patchiness of plant–fungus symbioses. Their broad phylogenetic distribution across Ascomycetes and their close but commensal association with living plant hosts made them excellent candidates to address several underlying assumptions in research on the ecology of fungal symbionts of tropical trees.

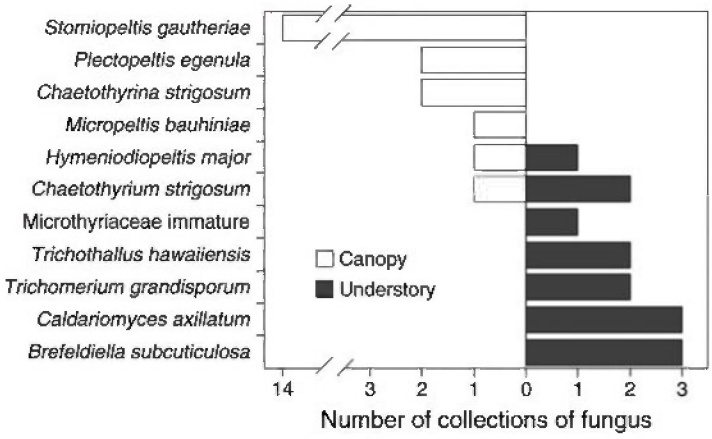

FIG. 2. Distribution of epifoliar fungal symbionts in the canopy (open bars) and understory (solid bars) on *Cleistanthus myrianthus* (Euphorbiaceae) in Cape Tribulation, Australia.

First, because the rarity of most tree species in tropical forests makes reliable encounter difficult, fungal symbionts in diverse rainforests should be polyphagous (May 1991). However, the complexity of interactions between plant and fungal symbionts means extreme generalism is also unlikely. It is often assumed that fungi are more likely to share closely related hosts, so that the probability of sharing hosts declines with increasing phylogenetic distance between hosts (Webb et al. 2006). For instance, host-range testing for the safety of potential bioherbicide pathogens is based largely on the centrifugal phylogenetic method of host selection (Wapshere 1974, Briese 2003). For epifoliar fungi, we found that fungi were polyphagous, colonizing hosts from a diversity of plant lineages, but that contrary to expectation we detected no phylogenetic signal in the observed host range. Whether more intimate pathogenic or mutualistic symbioses show phylogenetic signal needs to be rigorously tested.

Second, common plant species were more likely to harbor and share fungal species than were rare species, likely a function of common hosts more efficiently sampling the local mycota. If we assume a neutral model that fungi are host non-selective and able to colonize any host species encountered in an appropriate environment, then more common hosts will simply accumulate a greater richness of fungi as a simple species-area relationship. However, epifoliar fungi show host preferences, suggesting the possibility that common hosts "culture" their own symbionts in a density-dependent manner, or that other density-dependent agents (such as honeydew secreting insects) indirectly facilitate the growth of epifoliar fungi. In either case, propagules dispersing from those hosts can colonize suitable heterospecific hosts, and the likelihood that a particular tree species would encounter such spillover (Power and Mitchell 2004) should be proportional to its local abundance. Suitable common hosts could then provide additional density-dependent feedback, increasing the relative abundance of symbionts that share common hosts. In addition to opportunities of encountering hosts to which the fungus is pre-adapted, common hosts provide greater opportunities for the evolution of novel host–fungus associations (Parker and Gilbert 2004).

Third, environmental conditions have a strong controlling influence over the distribution and impacts of plant-fungal symbioses (Gillett 1962, Givnish 1999). We found strong vertical stratification for both overall abundance of epifoliar fungi and for particular fungal species. Vertical stratification is common in foliar plant pathogens and many other tropical taxa (Gilbert 1995, DeVries et al. 1997, Gilbert et al. 1997, Basset et al. 2001, García-Guzmán and Dirzo 2004). In the horizontal dimension, variation in canopy openness was a very strong predictor of the distribution of epifoliar fungi in the forest understory, as shown earlier for the epifoliar *Scolecopeltidium* (Gilbert et al. 1997).The patchiness of plant–fungal symbioses is clearly driven by environmental impacts on fungal growth as well as by the availability of suitable host species.

Finally, we found no evidence that adult trees act as reservoirs for fungal symbionts to infect nearby offspring, one of the assumptions of the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). For insects, Basset et al. (2001) found little evidence for exchange between canopy and understory for insects, and suggested canopy insects are likely resident habitat specialists, although Barone (2000) found that adults and juveniles of two rainforest tree species largely shared their suites of chewing herbivores. In our study, understory juveniles encountered a much more diverse suite of fungal symbionts than did their mature counterparts. This canopy–understory disconnection is important because although several studies have shown distance-dependent pathogen or mutualist patterns for soilborne organisms (Augspurger 1984, Newbery et al. 2000, Hood et al. 2004), to our knowledge none have yet demonstrated that the canopy serves as a reservoir for symbionts. Density of airborne fungal spores is many times lower in the rainforest canopy than the understory (Gilbert and Reynolds 2005), probably reflecting both reduced colonization of canopy leaves and environmental conditions hostile to spore production. Our data suggest that the dynamics of foliar fungal symbioses

with above-ground plant parts in the rainforest understory may be largely disconnected from dynamics in the canopy above.

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APPENDIX A

Canopy openness as a measure of microclimate at canopy and understory sample sites for radial transects in Cape Tribulation, Australia (*Ecological Archives* E088-035-A1).

APPENDIX B

Indentification and frequency of collection of epifoliar fungi in canopy or understory radial transects from Cape Tribulation, Australia, or San Lorenzo, Panama (*Ecological Archives* E088-035-A2).

APPENDIX C

Calculation of the probability of plant species being free of epifoliar fungi, under the assumption that fungi are host nonselective (*Ecological Archives* E088-035-A3).

APPENDIX D

Logistic regression results for the effect of phylogenetic distance (My), joint relative abundance (JRA), or the interaction (MyxJRA) on the probability that two plant species shared epifoliar fungal symbionts, from radial transects at San Lorenzo, Panama, and Cape Tribulation, Australia (*Ecological Archives* E088-035-A4).

APPENDIX E

Logistic regression results for the effect of canopy fungi (presence/absence of fungi on nearest mature conspecific), juvenile density (number of juveniles in 3-m radius around adult), and percentage of canopy openness on the proportion of juvenile *Cleistanthus myrianthus* colonized by epifoliar fungi at Cape Tribulation, Australia (*Ecological Archives* E088-035-A5).