

Factors related to diversity of decomposer fungi in tropical forests

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Recent studies suggest that host-preferences are common among certain groups of tropical fungal decomposers but rare in others, and sometimes occur where we least expect them. Host preferences among microfungi and ascomycetes that decompose leaf litter are common but usually involve differences in relative frequencies more than presence/absence, so their diversity may be loosely correlated with species richness of host trees. Strong host-specificity appears to be rare among wood decomposer fungi, whereas characteristics of their substrata and habitat are very important for this group. Anthropogenic disturbance predisposed a tropical forest to subsequent hurricane damage, and the resulting direct and indirect effects on host diversity and habitat heterogeneity were reflected in the decomposer fungal community more than sixty years after the original disturbance. While species richness of dictyostelid slime molds and functional diversity of their bacterial prey increased with disturbance, the more diverse microfungi and ascomycetes were apparently negatively affected by disturbance.

Keywords: fungal diversity; tropical forests; decomposers; anthropogenic disturbance; natural disturbance.

Introduction

Fungal diversity has received increasing attention during the last decade in part because fungi are used for production of antibiotics, enzymes, and food, and as agents for biopulping of paper and bioremediation of chemical spills (Hawksworth, 1991, 1993; Hawksworth and Colwell, 1992; Nisbet and Fox, 1991). Although temperate mycotas are relatively better known than tropical ones, fungal diversity is generally thought to be greater in the tropics and subtropics than at higher latitudes, especially among taxonomic groups dominated by decomposers (Lodge *et al.*, 1995). The reasons for higher diversity at low latitudes are not always clear, but the consensus of mycologists with experience in more than one hemisphere is that host diversity, resource abundance and habitat diversity are important contributing factors (Lodge *et al.*, 1995). Although decomposers might be expected to exhibit less host-specificity or host-preference than pathogens and beneficial symbionts, the survey suggested that diversity in certain groups of decomposer fungi is strongly related to host diversity (Lodge *et al.*, 1995).

The methods used to inventory fungi are inherently labour-intensive and many years of collecting are required to encounter the numerous larger species that only rarely produce

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fruiting structures (Watling, 1995; Ammirati, O'Dell and Lodge, unpublished). Therefore, understanding the causal and correlative factors that are related to fungal diversity may be especially helpful in suggesting which threatened areas are likely to support a high diversity or a unique group of fungal species, and are therefore of greater value in conservation efforts (Lodge *et al.*, 1995). In addition, knowledge of which factors are important in organizing fungal communities is essential for designing more efficient sampling strategies, whether it is for the purpose of bioprospecting or for inventory, monitoring and conservation. Attempts to inventory highly diverse taxa in which samples from different habitats have been combined often result in species discovery curves that do not or only slowly reach an asymptote, and distributions that are not lognormally distributed and are therefore difficult to analyse (Coddington *et al.*, 1991). Finally, understanding how natural and anthropogenic disturbances influence fungal diversity may help us to better manage and protect these economically valuable resources.

The purpose of this paper is to summarize results from some recent research that advance our understanding of the factors related to diversity of decomposer fungi in tropical forests. The following questions are specifically addressed. To what degree do tropical decomposer fungi have preferences for particular hosts or groups of hosts, types and diameter classes of their substrata, position of their substratum relative to the ground, and states of substratum decay? Secondly, for how long do natural and anthropogenic disturbances leave their impressions on fungal decomposer communities?

Results from recent research

Substratum preference

Tropical decomposer fungi are frequently restricted to particular size classes and types of substrata (Hedger, 1985; Lodge, 1996). For example, an analysis of the data presented in Lodge (1996) shows that almost all decomposer fungi were restricted to one or at most two similar types of substrata at El Verde in the Luquillo Mountains of Puerto Rico. Substrata were divided into the following classes: logs (> 10 cm diameter), branches (> 1 cm to 10 cm), twigs (< 1 cm), leaves (including petioles), roots, and soil (Lodge, 1996). Some of these fungi might have appeared to be restricted to particular substrata because they were only collected once or a few times, but they often had opportunities to colonize other types of substrata that were in contact with their own. Of the 705 decomposer fungi, 493 spp. (70 %) were restricted to one substratum (246 spp. were only on leaves, 43 in soil, 13 on roots, 27 on twigs, 84 on branches and 80 on logs). A further 173 species (25 %) were found only on two similar substrata (84 on logs and branches, 34 on branches and twigs, 28 on twigs and leaves, 21 on roots and wood, and 16 in soil and one other substratum). In contrast, only 39 species (5 %) were found on three or more substrata (12 on logs, branches and twigs, 15 on branches, twigs and leaves, and 12 on soil and two other substrata). These results are consistent with the level of substratum specificity found by Holler and Cowley (1970) at El Verde in which 53 of the 77 species cultured from soil were not found in either roots or surface litter.

Microhabitat preference

A recent survey by S.M. Huhndorf at El Verde in Puerto Rico (Huhndorf and Lodge, unpubl. data) showed that many wood-inhabiting ascomycetes had distinct preferences for the state of substratum decay and position relative to the ground, in addition to sub-

stratum type and diameter class. Such preferences have also been noted for tropical wood decomposer fungi in Africa (Ryvarden and Nuñez, 1992; Laessøe *et al.*, 1996). Similarly, Hedger (1985) showed that, in Ecuador, leaf decomposer basidiomycete fungi from the lower litter required partially decomposed leaves, in contrast to agarics of the upper layer that required freshly fallen leaves. Thus the availability of different microhabitats and substrata in different states of decay are likely to influence the diversity of decomposer fungi in tropical forests. Such factors have been discussed in greater detail in Hedger (1985), Lodge and Cantrell (1995) and Laessøe *et al.*, (1996).

Host preference

Agarics that decompose fallen leaves only rarely show strong host-specificity, and then it is usually for broad classes of hosts such as monocotyledonous versus dicotyledonous plants in the tropics, or gymnosperms versus angiosperms in temperate forests (Hedger, 1985; Lodge, 1993; Watling, 1995). Specificity occurs slightly more commonly among fruit-inhabiting agarics, such as those that are specialized on cones of conifers or infructescences of *Magnolia* spp. In contrast, larger ascomycetous fungi in the Xylariaceae (e.g. dead man's fingers) are very frequently restricted to fruiting on leaves and fruits of particular host plant genera or families in the tropics. For example, in Puerto Rico, Laessøe and Lodge (1994) and Laessøe, Lodge and Rogers (unpublished results) found that over half of the thirteen species of *Xylaria* on leaves and fruits were restricted to a single host plant genus or family (i.e. *X. aristata*, *X. axifera*, *X. meliacearum*, *X. phyllocharis* and *X. stromatica* on leaves; *X. warburgii* and *X. palmicola* on fruits were host-specific, whereas *X. apiculata*, *X. appendiculata*, *X. clusiae*, *X. ianthinovelutina* on leaves and, *X. mellisii* and *X. multiplex* on fruits showed no strong preferences). Gonzalez and Rogers (1989) have similarly found that a high proportion of the *Xylaria* species growing on fruits in Mexico are host-specific.

Microfungi growing in decomposing plant debris are mostly vegetative or asexually reproducing states of ascomycetes. In a study of specificity among leaf decomposers in Puerto Rico, microfungi were cultured from decomposing leaves of two tree species, *Manilkara bidentata* (Sapotaceae) and *Guarea guidonia* (Meliaceae), that occurred together on the forest floor at two widely separated sites (Polishook *et al.*, 1996). As in the xylariaceous ascomycetes, which represented ca. 6% of the 338+ species of microfungi isolated from the leaf litter by Polishook *et al.* (1996), slightly more than half of the 172 microfungal species that were cultured at least twice were restricted to one of the two leaf species (58%). Such host preferences among leaf decomposer fungi have previously been found by Cowley (1970) in Puerto Rico and Cornejo *et al.* (1994) in Panama. Cowley (1970) placed leaves of six tree species at two sites, and found a greater similarity in fungal assemblages between leaf litter of the same species located at different sites than between leaves of different species located at the same site. Cornejo *et al.* (1994) compared fungi isolated from decomposing leaves of five tree species and also found host preferences.

Bills (in Polishook *et al.*, 1996) hypothesized that much of the host preference exhibited by microfungal decomposers may be related to physical and chemical characteristics of leaves rather than host-specificity in the taxonomic sense (i.e., for a single host species, genus or family). A total inventory of microfungi in litter therefore might be obtained without having to culture fungi from leaves of every tree species in the forest – a daunting task in lowland tropical forests that have a high diversity of trees. Host preference in leaf decomposers is often quantitative rather than qualitative; in all of the studies cited above,

differences in relative abundances between fungal assemblages were greater than differences in fungal species composition among leaf litter species. The diffuse nature of host preferences make the relationship of species richness between trees and decomposer fungi difficult to analyse. Nevertheless, knowledge of the importance of host-preference in structuring fungal decomposer communities is useful for optimizing sampling strategies for both bioprospecting and for obtaining complete inventories (Polishook *et al.*, 1996). For example, Bills and Polishook (1994) had previously used random grab samples of decomposing leaves in a rain forest in Costa Rica, but the overlap in fungal species composition among their samples was so small that the only conclusion which could be drawn was that total species richness could not be estimated because the community had been undersampled (Bills and Polishook, 1994; Lodge and Cantrell, 1995).

Although it is reasonable to hypothesize that much of the host preferences expressed by leaf decomposer fungi are attributable to species that start out as pathogenic or non-pathogenic inhabitants (i.e. endophytes) of living leaves, there is little evidence to support this view. Endophytic fungi were cultured by Lodge *et al.* (1996) from young, healthy leaves of *Manilkara bidentata* trees located directly above one of the decomposition plots used by Polishook *et al.* (1996), but only five of the 23 fungal endophyte species were also found among the 204+ fungi in decomposing *Manilkara* leaves. In other words, only 22 % of the endophytes remained in the decomposing leaves, and these represented ca 1 % of the fungal decomposers. Furthermore, three of the five species found in live and decomposing leaves were *Xylaria* species that are known to have broad host ranges (Laessøe and Lodge, 1994), and only the two remaining species are likely to be host-specific (i.e. *Phyllosticta sapotae* and *Phomopsis manilkarae*; Lodge *et al.*, 1996). Possibly more species common to living and decomposing leaves would have been found if older leaves had been used in the endophyte study, but it is unlikely that these represent a large fraction of the decomposer community. The results of Polishook *et al.* (1996) and Lodge *et al.* (1996) are consistent with those of Laessøe and Lodge (1994), who found that species of *Xylaria* that were host-specific on decomposing leaf petioles were not in live petioles, but that xylariaceous endophytes that were recovered from live petioles had broad host ranges.

In contrast to the pattern of strong host-preference among tropical ascomycetes and microfungi that decompose leaf litter, there is a low frequency of host preferences among tropical wood decomposer fungi. Huhndorf (unpubl. data) found that only one of the 350+ species of non-xylariaceous ascomycetes on wood at El Verde in the Luquillo Mountains was host-specific, i.e., *Schizoparme botrididis* on *Buchenavia capitata* (Combretaceae). Similarly, only three to seven of the ca 120 species of xylariaceous ascomycetes that occurred on wood in Puerto Rico had restricted host ranges (Laessøe, Lodge, Rogers, and Huhndorf, unpubl. data). The species known to be host-restricted were *Camillea verruculospora* on *Miconia* spp (Melastomataceae) Lodge and Laessøe, 1995), *Xylaria guareae* on *Guarea guidonia* (Laessøe and Lodge, 1994) and *Rosellinia bunodes*, pathogen, on *Coffea arabica* and *Psychotria berteriana* (Rubiaceae) and *Hibiscus* (Malvaceae) (Lodge, 1996). In addition, five undescribed *Anthostomella* spp (a group that is often host-specific) were found only once by Huhndorf (unpubl. data) at El Verde in Puerto Rico, and these might eventually prove to have host preferences. Although the frequency of host-specificity in polypore (basidiomycete) wood decomposers is also likely to be low, the role of host diversity in contributing to the diversity of this group cannot be discounted (Lodge *et al.*, 1995).

Estimates of fungal diversity

Our estimates of global fungal diversity are often based on extrapolations from better known temperate ecosystems to poorly known tropical ones. For example, because the fungi and plants in the British Isles were more thoroughly known, (Hawksworth, 1991) used the highest ratio of fungi to phanerogamic plant species (6:1) from a variety of comparisons to predict the number of all fungi in the British Isles and then to estimate that there were at least 1.5 million species of fungi in the world. The robustness of such extrapolations depends on consistency of ratios of phanerogams to fungi among different ecosystems, and the average distribution ranges of phanerogams versus fungi (Hammond, 1992). Both of these assumptions are sensitive to regional differences in the degree of host-specificity in fungi.

May (1980, 1988) hypothesized that, among insects and other organisms that depend on plants, host-specificity is more frequent in temperate forests that have high tree species dominance and low diversity as compared to many tropical forests in which tree dominance is low and diversity is high. For example, species richness can exceed 400 tree species per hectare in some lowland tropical forests (Valencia *et al.*, 1994), and consequently host-specific fungi and insects may have difficulties in successful dispersal and colonization of their widely dispersed hosts. Despite the logic of May's (1988) hypothesis, several mycologists working in the tropics believe that Hawksworth's (1991) global estimate of 1.5 million fungal species is too low. For example, Smith and Waller (1992) estimated that there were at least one million fungal species on tropical plants alone based on their work in Brazil. Similarly, Pascoe (1990) estimated that there were at least ten times as many fungi as vascular plants based on work in Australia. The data summarized in this paper suggest that host-specificity and preferences sometimes occur where we would least expect it in tropical forests, such as among ascomycetes and microfungi that decompose leaf litter. Such host preferences can be so diffuse, however, that it will be difficult to establish the ratio of obligate fungi per plant host species in tropical forest.

Effects of natural and anthropogenic disturbances on microbial diversity

Biological legacies of anthropogenic and natural disturbances in tropical forests are being studied intensively at the Luquillo Long Term Ecological Research site in Puerto Rico. A 16-ha gridded forest plot in subtropical wet forest at El Verde in the Luquillo Mountains has different land use histories, of which the most recent human disturbance occurred more than 60 years ago (Zimmerman *et al.*, 1994). Previous anthropogenic disturbance favoured colonization by secondary tree species that were differentially more susceptible to damage from Hurricane Hugo in 1989 (Zimmerman *et al.*, 1994; Willig *et al.*, 1996). Leaf litter of the secondary tree species was also found to decompose more rapidly than the late secondary and primary forest species (Zou *et al.*, 1995). Willig *et al.*, (1996) studied the entire grid, including areas that had previously been clearcut, and found that the activity and functional diversity of bacteria (in terms of enzymatic diversity and their abilities to degrade different substrates) increased significantly with increasing disturbance. Because anthropogenic disturbance had predisposed those forest areas to the effects of a subsequent natural hurricane disturbance, these disturbance factors were so tightly correlated that their effects could not be separated (Willig *et al.*, 1996).

Other efforts to study microbial diversity in the forest grid at El Verde have contrasted one area that had 80–100 % forest cover (light charcoal cutting) with another that had 50–80 % forest cover (former shade coffee plantation) in the aerial photographs of 1936. In

addition to the increased functional diversity of bacteria in the more disturbed part of the grid (Willig *et al.*, 1996), there was an increase in species richness of dictyostelid slime molds, which primarily consume bacteria and are best described as predators of decomposers (Stevenson and Landolt, unpubl. data). Stevenson and Landolt (unpubl. data) cultured dictyostelids from leaf litter and found eight species in the area that had 50–80 % forest cover versus one species in the area that had over 80 % forest cover 60 years ago. It is not known how much the increase in habitat heterogeneity resulting from hurricane damage in the previously disturbed part of the grid contributed to dictyostelid diversity versus the correlated increased diversity of bacteria. Huhndorf (unpubl. data) found that some wood-inhabiting ascomycetes (e.g. two species of *Cercophora*) were restricted to the more disturbed part of the grid, and that these were generally ‘weedy’ widespread species that are commonly found in disturbed habitats. However, in contrast to bacteria and dictyostelid slime molds that were more speciose in the more disturbed part of the forest, Huhndorf also found more species of wood-inhabiting ascomycetes per sample in the least disturbed part of the grid. Although one might hypothesize that the higher diversity of tree species in the less disturbed forest contributed to greater ascomycete diversity, very few wood-inhabiting ascomycetes were strictly host-specific as discussed above. It is possible that subtle undetected preferences among wood-decomposer ascomycetes for groups of hosts could contribute to higher fungal diversity in more species-rich forest, as suggested for leaf decomposer fungi. Regardless of the controlling factors, preservation of some areas that have relatively undisturbed forest appears to be important for maintaining diversity of both wood and leaf decomposer fungi in the tropics.

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