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Relationship of host recurrence in fungi to rates of tropical leaf decomposition

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Summary

Here we explore the significance of fungal diversity on ecosystem processes by testing whether microfungal 'preferences' for (i.e., host recurrence) different tropical leaf species increases the rate of decomposition. We used pairwise combinations of γ-irradiated litter of five tree species with cultures of two dominant microfungi derived from each plant in a microcosm experiment. The experiment was designed to test whether early leaf decomposition rates differed depending on relationships between the leaf litter from which the fungi were derived (i.e., the source plant) and the leaf substrata decomposed by these fungi in microcosms. Relationships tested were phylogenetic relatedness between the source and substratum leaves, and similarity in litter quality (lignin, N and P) between the source and substratum. We found a significant interaction between microfungi and leaf species ($P < 0.0001$), and differences among the four classes of source–substratum relationships were highly significant ($P = 0.0004$). Combinations in which fungal source leaves were of the same species or family as the substratum, or the fungal source resembled the substratum in quality had marginally faster decomposition than when the fungal source and substratum leaves were mismatched (i.e., unrelated and of dissimilar quality). In some microcosms, a basidiomycete contaminant had a strong additive effect on decomposition of *Croton poecilanthus* leaves resulting in faster decomposition than with microfungi alone ($P < 0.0001$). Comparisons among leaf–microfungal combinations were made after the effect of the basidiomycete covariate was adjusted to zero. The data on microfungi suggest differential abundance in particular hosts, which

contributes to species diversity of decomposer fungi in tropical forests, affects rates of decomposition.
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Introduction

The role of biodiversity in determining rates of ecosystem processes is controversial. Degens (1998) found no change in the rate of decomposition with reduced microbial functional diversity. In contrast, Naeem et al. (2000) found a positive correlation between number of microbial species and decomposition, which Morin (2000) attributed to greater numbers of functional groups. Goubière and Corman (1987), Kjøller and Struwe (1987), Rosenbrock et al. (1995) and Cox et al. (2001), however, showed that certain fungi play pivotal roles in controlling rates of leaf decomposition of different resource components. Pivotal microbial species might thus be more important than number of species or functional groups per se in controlling decomposition.

The diversity of fungi in decomposing leaves in the tropics is very high (Bills and Polishook, 1994a, b; Cornejo et al., 1994; Polishook et al., 1996; Paulus et al., 2003). This is in part because many microfungal species in decomposing leaves are recurrent on particular host plants (Polishook et al., 1996; Lodge, 1997) and at particular stages of decomposition (Cornejo et al., 1994; Westover et al., 1997; Watkinson, 1998; Promputtha et al., 2002; Yanna Ho and Hyde, 2002; Zhou and Hyde, 2002); such arrangement tend to be the rule rather than the exception. Microfungi are primarily asexual states of fungi in the Ascomycotina and Zygomycotina. In contrast, macrofungal decomposers, such as mushrooms (Basidiomycotina, Agaricales), show little discrimination among leaf species in the tropics (Lodge, 1997). Many studies have shown that microfungi are differentially abundant in particular plant species (referred to as host recurrence by Zhou and Hyde, 2001; and host selectivity by Hooper et al., 2000) or types of substrata in tropical forests (Cowley, 1970; Polishook et al., 1996; Lodge, 1997; Yanna Ho and Hyde, 2001; Zhou and Hyde, 2001). Bills (1994), Polishook et al. (1996), Wong and Hyde (2001) and Zhou and Hyde (2001) suggested that patterns of host-exclusivity and -recurrence might be explained by responses of decomposers to differences in physical structure and nutrient levels among host plants. Nevertheless, no studies in tropical areas have focused on understanding the ecological significance of such 'preferences' by decomposer

microfungi for particular plant substrata, i.e., whether differentially abundant fungi decompose their 'preferred' substratum faster than fungal dominants from other plant substrata.

Microcosm experiments have been found to be useful for testing factors that influence decomposition under controlled conditions (Taylor and Parkinson, 1988a, b; Cortez et al., 1996; Mikola and Setälä, 1998a, b; Conway et al., 2000; Naeem et al., 2000). In this study, we used a microcosm experiment to test the role of interactions between particular plants and fungi on decomposition rates. Each microcosm contained sterilized (γ irradiated), senescent leaves of one of the five leaf species and a dominant, early stage decomposer microfungus cultured from one of the leaf types. Five plant species and 10 fungal species (two dominants from each of the leaf types) were used in all possible combinations. We hypothesized that under constant environmental conditions, plant and fungal species interactions would control rates of litter decomposition. Specifically, we hypothesized that fungi that were dominant in a particular leaf species would decompose those leaves faster than fungal dominants from other leaf species. Similarly, we hypothesized that fungi would more quickly decompose leaves of plants that were closely related taxonomically, or were chemically and structurally similar to the leaves in which they were dominant. Weight loss was used as response variable for the interaction between fungal decomposers and leaf substrata.

Materials and methods

Plant species selection and early decomposition

Selection of leaf species was based primarily on phylogenetic relationships, litter quality (nitrogen, phosphorus and lignin content), and presence or absence of latex (Table 1). *Croton poecilanthus* Urb. and *Sapium laurocerasus* Desf. both belong to the Euphorbiaceae, but *C. poecilanthus* leaves are lower in quality. *Croton poecilanthus* and *Manikara bidentata* (A. DC.) A. Chev. leaves have similar chemical and physical traits including the presence of latex, even though the latter belongs to a

Table 1.   Selected tree species combinations for comparisons based on leaf phylogenetic relatedness and litter quality

Leaf phylogenetic relationship	Leaf quality	
	Same or similar	Different
Same or related species	**1** All five spp. with self; *Inga vera* and *Inga fagifolia*	**3** *Sapium laurocerasus* and *Croton poecilanthus*
Different family	**2** *Croton poecilanthus* and *Manilkara bidentata*	**4** All other species pairs (seven mismatched pairs)

Note: The two-by-two table describes the relationship between the substrata that were decomposed in the microcosm experiment and the fungal source leaves. The assigned cell numbers in bold are referred to for contrasts in subsequent statistical analyses.

different family (Sapotaceae). *Inga vera* Willd. *I. fagifolia* (L.) Willd. (= *I. laurina* (Sw.) Willd.) in the Fabaceae were selected to represent two closely related leguminous species with high lignin and nitrogen concentrations, though differing slightly in concentrations of secondary plant compounds. Leaves dried at 65 °C were analyzed for nitrogen (N) and phosphorus (P) at the International Institute of Tropical Forestry in Puerto Rico using a direct current Beckman plasma atomic emission spectrometer (Spectra Span V). Leaves dried at 60 °C were analyzed for lignin or lignin-based compounds at The Natural Resources Research Institute in Minnesota.

Freshly fallen senescent leaves of the selected species were collected the same day they abscised and used fresh to represent the normal substrata for primary fungal decomposers. A subset was oven dried to obtain wet to dry weight ratios. Litterbags (20 × 20 cm^2) made of 2 mm mesh plastic screening containing 5 g of a single species were placed on top of the litter layer in the field at the end of July 2000 under their corresponding source trees for 5 weeks to allow colonization by their normal decomposers. Four bags were placed under each of the five trees for each of the selected plant species to allow for heterogeneity among sites; trees of the same species were at least 100 m apart. After 5 weeks, leaves from 15 litterbags per species were oven dried at 65 °C for 72 h and weighed to determine percent moisture and weight loss. Weight loss at 5 weeks decomposition was near 40–50% in *S. laurocerasus* leaves, and between 10% and 20% in the other leaf species. A pooled sample comprised of one randomly chosen litterbag from each tree location was used for isolation of fungi.

For comparison of relative rates of decomposition among the selected leaf species under normal field conditions, five replicate litterbags of each leaf species (as described above) were placed in a common plot under *Dacryodes excelsa* Vahl., and left to decompose for 12 weeks. None of the source tree species were present in the common plot. Leaves were oven dried at 65 °C for 72 h and weighed to determine percent weight loss after 12 weeks.

Fungal isolations to determine the dominant early decomposer fungi

To determine which early decomposer fungi were vegetatively dominant, we used the particle filtration method as described by Bills and Polishook (1994a, b) and Polishook et al. (1996), and modified by Bills (2000). A trial with different dilutions of *S. laurocerasus* leaves that had been decomposed for 5 weeks was used to find the dilution that yielded the highest diversity of fungal species (1:100). Diversity was compared among dilutions using rarefaction curves (Bills and Polishook, 1994b).

To select the two dominant fungi from each leaf species for the microcosm experiment, leaves that had been decomposed for 5 weeks, as described above, were air dried for 3 h to facilitate pulverization, pooled among the five replicate litter bags, and pulverized in a sterilized blender. A 5 g subsample was processed according to Bills and Polishook (1994a, b). Particles were plated on malt-Cycloporin agar and Bandoni's medium that inhibit growth of bacteria. All fungal colonies growing from particles (ca. 30–60 colonies per plate) were transferred to slants malt yeast agar in 90 mm Petri dishes, and then subcultured onto oatmeal agar, corn meal agar, malt agar, malt yeast agar and potato dextrose agar (Rossman et al., 1998). Autoclaved leaves of banana (*Musa* sp.) or the source plants were added to agar media to promote fungal sporulation. The water from the final

washing of the particles was also plated on malt-Cycloporin Agar and Cyclosporin A, and this confirmed that essentially all of the fungal spores had been removed by the washing.

Primary sorting of colony morphotypes was based on colony color, surface texture, rate of growth; color changes in of the agar media; and type, color, size and ornamentation of conidiophores and conidiospores. Classification of morphotypes was reviewed at 2 and 4 months, and the fungi were arranged by their rank abundance based on frequencies of occurrence. Selection of two dominant fungal species each leaf species was made from the three most frequent morphotypes. Some dominants were not selected because they were also dominants in the other leaf litter species, or their airborne spores posed a risk of cross-contamination and were a health hazard. We identified to genus the 10 most abundant morphotypes in each leaf species using Carmichael et al. (1980), Malloch (1981), Barnett and Hunter (1998) and Watanabe (2002). Further identification was done by us (*Colletotrichum gloeosporioides*), P. Bayman at UPR-RP (*Aspergillus niger*) and C. Deacock at BCC/MUCL (*Aureobasidium pullulans*, *Fusarium solani*, *Volutella concentrica*) using specialized literature and reference cultures. The selected fungal isolates and the other eight most frequent isolates from each leaf litter species appear in Table 2.

Microcosm experiment

Translucent plastic containers with tight fitting lids ($19 \times 12 \, cm^2$ and 8.5 cm deep) were modified with a ventilation tube and a wire mesh shelf covered with autoclaved muslin for use as microcosms. The wire shelf kept the litter 3 cm above the bottom of the container. The microcosms were sterilized with a 0.5% solution of sodium hypochlorite for 10 min followed by a rinse with 70% ethanol in water; finally, these were exposed to a UV light in a sterile hood for 12 h. The end of each ventilation tube was sealed with paraffin film to prevent contamination by fungal spores and mites.

Senescent and freshly fallen leaves were collected, air dried and irradiated twice with γ-rays, 3640 rad of Cs^{137} at first, and then 4090 rad a month later. Culturing on malt yeast agar showed that some microfungi survived the first but not the second irradiation. Five grams of whole, sterile leaves of a single plant species were placed in each microcosm, moistened with sterile distilled water, and inoculated with 10 agar plugs (5 mm diameter and deep; malt agar) from a clean culture of one

Table 2. The 10 most vegetatively dominant, early-stage decomposer microfungi cultured from leaves of five tropical tree species are listed according to decreasing frequency

I. fagifolia (IF) 182	I. vera (IV) 250	M. bidentata (MB) 294	C. poecilanthus (CP) 281	S. laurocerasus (SL) 228
Aureobasidium cf. pullulans (IF1)	**Nectria sp. 2 (IV1)**	**Pestalotiopsis sp. (MB1)**	**Diplopodia sp. (CP1)**	**Fusarium solani (SL1)**
Fusarium solani	**Phoma sp. (IV2)**	**Colletotrichum sp. 2 (MB2)**	**Volutela concentrica (CP2)**	**Trichoderma sp.**
Cladosporium sp. (IF2)	**Aspergillus niger**	**Trichoderma sp.**	Pestalotiopsis sp.	**Mucor sp. (SL2)**
Nectria sp. 1	Diplopodia sp.	Volutela concentrica	Aspergillus niger	Penicillium sp.
Pestalotia sp.	Nectria sp. 1	Aspergillus sp.	Aspergillus sp.	Colletotrichum gloeosporiodes
Colletotrichum sp.	Mucor sp.	Xylaria sp. 3	Colletotrichum gloeosporiodes	Pestalotia sp.
Curvularia cf.	Pestalotia sp.	Phomopsis sp.	Phomopsis sp.	Nectria sp. 1
Phomopsis sp.	Rhizopus sp.	Penicillium sp.	Nectria sp. 2	Rhizopus sp.
Trichoderma sp.	Xylaria sp. 2	Aspergillus sp. 1	Xylaria sp.	Phomopsis sp.
Xylaria sp. 1	Unidentified	Aspergillus sp. 2	Trichoderma sp.	Xylaria sp.

Note: Leaves were allowed to decompose for 5 weeks under their source trees prior to culturing. The total number of cultures appears below each leaf species. Species in bold were used in the microcosm experiment (species code in parentheses).

fungal species and 1 ml of malt yeast liquid medium containing the same fungus. Agar plugs were cut using the large end of autoclaved disposable pipettes and transferred with flamed needles, while liquid cultures were dispensed using sterile large-diameter pipettes. The agar plugs and liquid medium were distributed evenly on the leaves; no excess liquid medium drained from the litter. The five leaf species were inoculated with two dominant decomposer fungi from each of the five leaf species in all possible combinations. There were three replicates for each of the 50 treatment combinations giving a total of 150 microcosms. Plant species were assigned a code corresponding to the first letter of genus and species. Fungal species were assigned the plant code from their source leaf followed by the number 1 or 2 according to their relative ranks (e.g., MB1 and MB2 from *M. bidentata*).

Numbers were assigned to the 150 microcosms randomly to randomize the placement of treatment combinations during incubation. The leaves were incubated at ca. 22 °C with a 12 h photoperiod for 17 weeks on a lab bench. Once per week, each microcosm was transferred to a sterilized laminar flow hood, opened and misted with 70 ml of sterile deionized water; leachates were then extracted from the bottom using a sterile syringe. At the end of the experiment, fruiting in the microcosms and in cultures of the remaining leaf material showed that eight of the 30 microcosms with *C. poecilanthus* had ligninolytic agaric basidiomycetes in addition to the microfungus they were inoculated with (one with *Marasmius* sp., and seven with *Melanotus eccentricus* (Murrill) Sing.).

Statistical analyses

Weight losses of leaves in the microcosm experiment described above were used as the measure of leaf decomposition for these analyses. Basidiomycete influences were evaluated using analysis of covariance (ANCOVA) methods (Milliken and Johnson, 2002) to determine if differences existed between replicates with and without basidiomycetes, and if so, to account for those differences in the analyses. Initially, a regression model was evaluated with a dichotomous variable (Littell et al., 1996; SAS Institute Inc., 1999, SAS V8.2, 2001) indicating the presence or absence of ligninolytic basidiomycetes to determine if their presence in some microcosms with *C. poecilanthus* leaves was significant. A significant non-zero basidiomycete effect on mass loss was detected for islolates CP2, IF1 and MB2, but not for leaves inoculated with isolates CP1 and IV1. A two-slope ANCOVA model was therefore used to account for the effect of basidiomycete contaminants, allowing for adjustment of the effect (Milliken and Johnson, 2002). Residual plots were examined to assess model assumptions.

Mean comparisons of weight losses were broken down to look at differences among plants, and among microfungi within each plant after the effect of basidiomycetes was removed. Comparisons were similarly made between plant–fungus combination groups according to whether the fungal source leaves and plant substrata were matched by phylogenetic relatedness or by leaf quality (Table 1). Following methods outlined in Westfall et al. (1999) each set of comparisons was considered to be a family of comparisons that were compared using the simulation adjustment method (using macros available from SAS®).

Weight losses of leaves that were decomposed in the field were evaluated using one-way ANOVA and post hoc Tukey's honestly significant difference (HSD) comparisons. Nitrogen, phosphorus and lignin concentrations were compared among leaf species using a fully factorial MANOVA and the General Linear Model followed by post hoc Tukey HSD comparisons. Residual plots were examined to assess model assumptions.

Results

Differences in fungal dominants among leaf species

The frequency of overlap among the top 10 fungal dominants between pairs of leaf species ranged from 1 to 5, and the mean percent overlap was 32% (Table 2). While the overlap in fungal species composition of the dominants in related leaves of different quality was relatively high (four of the 10 for *S. laurocerasus* and *C. poecilanthus*), the two *Inga* spp. had only one fungal dominant in common despite having similar leaf quality and belonging to the same genus. Although the plants from different families that were paired by leaf quality, *C. poecilanthus* and *M. bidentata*, had a relatively high overlap in fungal dominants (five of the 10), two pairwise comparisons between unrelated leaves of different quality also had high overlap in their fungal dominants. Despite being unrelated and having contrasting leaf quality, *I. vera* and *S. laurocerasus* shared four of the 10 fungal dominants, while *I. fagifolia* and *S. laurocerasus* shared five.

Leaf quality, characteristics and relative rates of decomposition

Nitrogen, phosphorus and lignin concentrations were compared among the five leaf species using one-way ANOVA followed by Tukey tests for pair-wise comparisons (significant differences at $P < 0.05$). The two species of *Inga* resembled each other closely in having very high concentrations of both lignin and N (differences not significant; Table 3). Although *M. bidentata* and *C. poeci-lanthus* are in different families (Sapotaceae and Euphorbiaceae, respectively), they are both char-acterized by the presence of latex, and had similar, intermediate concentrations of N and lignin (differ-ences not significant; Table 3). Differences in P

concentrations between *Manilkara bidentata* vs. *C. poecilanthus, and I. vera* vs. *I. fagifolia* were not significant. Although belonging to the same plant family (Euphorbiaceae), *C. poecilanthus* and *S. laurocerasus* leaves differed significantly in their concentrations of lignin, N and P (Table 3).

Decomposition rates are an indicator of leaf quality, and were compared with separate analyses for the microcosm and field experiments. Patterns of mass loss in the microcosms after 17 weeks were similar to those in the field after 12 weeks of decomposition (Fig. 1). Mass loss after 12 weeks in a common plot was greatest in *S. laurocerasus*, the leaf with the highest quality, and least in the two species with the highest concentrations of lignin (*Inga* spp.), and also in *M. bidentata* which had

Table 3. Leaf litter characteristics that were used to group species by litter quality for statistical comparisons

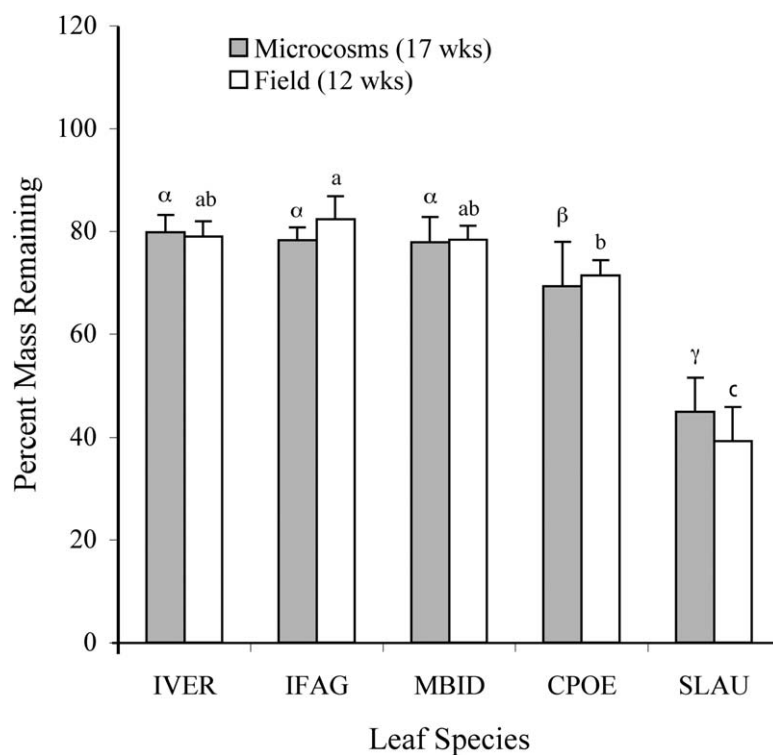| Plant	Lignin (%)	Latex	N (%)	P (%)
Inga vera	33.7	−	1.9	0.35
Inga fagifolia	30.7	−	1.8	0.26
Manilkara bidentata	16.3	+	0.8	0.25
Croton poecilanthus	17.8	+	0.6	0.11
Sapium laurocerasus	2.2	+	1.2	0.60

Figure 1. Mean percent mass remaining after 12 weeks of decomposition in the field in a common plot, and after 17 weeks decomposition in microcosms. Separate ANOVA with post hoc comparisons were performed for the field and microcosm experiments; treatments with the same letter did not differ significantly at the $P < 0.05$ level. *r* Different letters above the bars indicate species that differed significantly at the $P < 0.05$ level.

intermediate lignin concentrations (Table 3, Fig. 1). Weight loss did not differ significantly among the three slowest species to decompose (*I. vera*, *I. fagifolia* and *M. bidentata*) after 17 weeks in the microcosms or after 12 weeks in the field (Fig. 1). *Croton poecilanthus* decomposed significantly faster than the previous three species, but significantly slower than *S. laurocerasus* in both the microcosm and field experiments.

Weight loss differences among treatment combinations in microcosms

An overall ANCOVA was performed first to determine if there was a plant by fungus interaction, after adjusting the basidiomycete effect to zero. Treatment means were then compared with treatment groupings based on the fungal source and substratum plant combinations laid out in Table 1. In the first set of linear contrasts, fungi from the same source plant species as the substratum and those from a source plant related to the substratum were grouped and contrasted with the remaining two cells individually. A subsequent set of pairwise contrasts was performed among all the individual cells in Table 1.

After 17 weeks of decomposition, there were significant differences in mass loss among the microcosm treatments ($P < 0.0001$). The overall ANCOVA (Table 4) showed significant differences in weight loss among plants and among fungi, and more importantly for this study, the interaction of fungi and plants. Mean mass loss ranged from a maximum of 60% in *S. laurocerasus* to a minimum of 16% in *I. vera* (Fig. 1). A highly significant effect was also found for ligninolytic basidiomycete contaminants that accelerated decomposition of *C. poecilanthus* in some of the microcosms (Table 4). As noted previously in methods, the effect of basidiomycetes was significant in some microfungal treatments and not others, so subsequent analyses were done using modeling with two slopes to remove the effect of the basidiomycetes so that the original microfungal treatments could be compared. Of the 150 microcosms, 16 were found to

have microfungal contaminants at the end of the experiment. These were probably contaminated late in the experiment, and values for weight loss did not differ between microcosms contaminated with microfungi and uncontaminated replicates (*t*-tests). Data from microcosms with microfungal contaminants were therefore treated according to the fungi in the original treatment.

To test the original hypothesis that faster decomposition would result when leaves were decomposed by fungal dominants from plants that were phylogenetically related to the substratum, linear contrasts were constructed based on the ANCOVA model. For this hypothesis, fungi from the same source species as the substratum and those from a related leaf species (classes 1 and 3, respectively, from Table 1) were grouped. Microfungi from leaves of the same plant species or family as the substratum decomposed leaves marginally faster ($P = 0.0668$) than the corresponding means for those substrata. Fungal dominants from the same plant species (class 1) or a species related to the substratum (class 3) as a group decomposed the leaves marginally faster than fungi from unrelated leaves of a different quality (class 4; $P = 0.056$). When fungi from same plant or a plant species related to the substratum were compared to those from unrelated leaves of a similar quality than the substratum (classes 1 and 3 vs. 2), there was no difference in weight loss ($P = 0.687$). This suggests that matching of fungal substrata and sources based on leaf quality has an effect similar to matching by phylogenetic relatedness.

Overall differences among the four non-pooled classes of microfungal source–substratum relationships were highly significant ($P = 0.0004$). Leaves that were inoculated with fungi derived from a related plant that differed in quality from the substratum (class 3) than the overall mean, even though the source leaf species differed in quality from the substratum (Table 5). Leaves that were inoculated with fungi from unrelated leaves that differed in quality from the substratum (class 4) decomposed significantly slower than the overall mean (Table 5). The other two treatment classes did not differ significantly from the mean.

Table 4. Results of ANCOVA for treatments and interactions in the microcosm experiment

Effect	Numerator df	Denominator df	F-value	P-value
Plant	4	97	437.07	<0.0001
Fungus	9	97	3.47	0.0103
Plant × fungus	36	97	3.53	<0.0001
Basidiomycete covariate	2	97	32.37	<0.0001
Residual est. (σ^2) = 19.82		$N = 150$		

Pairwise comparisons between classes of source–substratum relationships and their effects on mass loss were made using two-sided tests and a familywise error rate of $P = 0.05$. All possible comparisons are given in Table 6, and those of particular interest for this study are noted below. When comparisons were restricted to leaf substrata that were related to the microfungal source leaves, substrata with fungal dominants from leaves that had the same or a similar quality (class 1) decomposed leaves significantly faster than fungi from leaves of dissimilar quality (class 3; Tables 6 and 7). When comparisons were restricted to leaf substrata that differed in quality from the fungal source leaves, fungi from related plants (class 3) decomposed the leaves significantly than fungi from unrelated plants (class 4; Table 6). Furthermore, fungi from related plants of dissimilar quality from the substratum (class 3) decomposed leaves faster than fungi from unrelated plants that had been matched by quality to the substratum (class 2; Tables 6 and 7).

Since the plant by fungus interaction was significant in the overall ANCOVA, each plant species was then analyzed separately to determine which plants contributed to this result. Plant by fungus interactions were statistically significant only for *C. poecilanthus* ($P < 0.0001$) and *S. laurocerasus* ($P = 0.0014$) leaves (Figs. 2a and b, respectively), though we also illustrate fungal source–substratum relationships for the two species of *Inga* (Fig. 2c, Table 7). Fungal dominants from leaves of different plant families that also differed in quality from the substratum caused slower decomposition in *C. poecilanthus* leaves than fungi that were matched to the substratum by phylogenetic relatedness or quality (Fig. 2a, Table 7). In *S. laurocerasus* leaves, fungi that were completely mismatched to the substratum decomposed leaves slower than fungal dominants from the same plant family as the substratum, even though the source differed in quality from the substratum, but not faster than fungi from *S. laurocerasus* (Fig. 2b). Though not statistically significant, fungi that were completely mismatched to the two *Inga* substrata decomposed the leaves slower than when the fungi were matched to the substrata by phylogenetic relatedness and quality (Fig. 2c).

The five fungal treatments that caused the fastest decomposition in *C. poecilanthus* leaves (MB1, CP1, SL1, SL2 and IF2) were significantly different from the two slowest fungal treatments (IF1 and IV2). The four treatments that caused the greatest mass loss in *C. poecilanthus* all came from leaves that were matched to the substratum by relatedness or quality (classes 1, 2 or 3), while four of the six slowest decomposers were completely mismatched to the substratum (class 4, Fig. 3e).

Performance of individual decomposer microfungi on the *S. laurocerasus* leaves fell into two partially overlapping groups not as easily distinguished as those in *C. poecilanthus*. The only statistically significant differences in mass loss

Table 5. The least-squares estimates of mean deviations of each treatment group mean from the overall mean percent mass remaining are given, followed by the probability value for the test of the hypothesis that the deviations are zero (note that the effect of the Basidimycete covariate was adjusted to zero; 98 degrees of freedom)

Phylogenetic relationship	Leaf quality	
	Similar	Different
Same or related species	**1** +0.1023 $P = 0.8611$	**3** −5.0754 $P < 0.0001$
Different family	**2** −0.4852 $P = 0.6854$	**4** +0.7432 $P = 0.0215$

Note: The general contrast indicated there were highly significant differences among the groups ($P = 0.0004$).

Table 6. Pairwise comparisons of percent mass remaining in contrasting groups using Bonferroni adjustments as well as a simulation macro in SAS as described in Westfall et al. (1999) at a familywise error rate of 0.05

Group contrasts	P-value ($P > |t|$)				
	Estimate	Standard errors	Raw	Bonferroni adjustment	Simulation adjustment
1 vs. 2	−0.5875	1.4161	0.6791	1.0000	0.6791
1 vs. 3	−5.1778	1.4161	0.0004	0.0021	0.0016
1 vs. 4	+0.6409	0.8445	0.4497	1.0000	0.6745
2 vs. 3	−4.5902	1.8022	0.0124	0.0497	0.0401
2 vs. 4	+1.2285	1.3269	0.3568	1.0000	0.6263
3 vs. 4	+5.8187	1.3269	<0.0001	0.0002	0.0002

Note: Group number designations are given in Table 2.

Table 7. Summary of hypotheses and results

Hypothesis	Comparison	Statistical test	Result	Figures and tables
I. Leaf quality differs among species	Overall differences in N, P and lignin among five plant species	Fully factorial MANOVA and GLM with Tukey tests	Significant, $P<0.05$	Table 5
Quality is similar	Same genus (same/similar quality): *I. vera* and *I. fagifolia*: N and lignin		NS	Table 3
Quality is different	Same family: *C. poecilanthus* and *S. laurocerasus*: N, P and lignin		Significant	Table 3
Quality is similar	Different families: *M. bidentata* and *C. poecilanthus*: N and lignin		NS for N and lignin; Significant for P	Table 3
II. First level, overall hypotheses				
A. Weight losses differ among plant–fungus combinations	Overall	ANCOVA (basidiomycete effect adjusted to zero)	Significant, $P<0.001$	Table 4
Plants differ	Plant		Significant, $P<0.0001$	Table 4
Fungi differ	Fungi		Significant, $P=0.0103$	Table 4
Plant–fungus combinations differ	Plant × fungus		Significant, $P<0.0001$	Table 4
Effect of delignifying Basidiomycetes	Basidiomycete fungal presence/absence in *Croton poecilanthus*	ANCOVA	Significant, $P<0.0001$	Table 4
B. The four non-pooled classes of fungal source–substratum relationships differ	Four classes: fungal source–substratum	ANCOVA, linear contrast: Pairwise comparisons using two-sided test and familywise error rate of $P=0.05$	Significant, $P=0.0004$	Table 5
	1. Substratum and source same genus or species; quality similar or same			
	2. Substratum and source unrelated (different families); quality similar			
	3. Substratum and source related (same family); quality different			
	4. Substratum and source unrelated (different family), quality different			
III. Group contrasts testing hypotheses regarding leaf source–substratum quality and relatedness relationships on decomposition by microfungi				
A. Contribution of each plant species to significant plant × fungus interaction, from II. A	Plant × fungus within plant species	ANOVA	*C. poecilanthus*, $P<0.0001$ *S. laurocerasus*, $P=0.0014$ *Inga* spp. same trend, NS *M. bidentata*, NS	Fig. 2a and b; *Inga* 2c

Table 7. (*continued*)

Hypothesis	Comparison	Statistical test	Result	Figures and tables
B. Relatedness hypothesis, from II. A: Fungi from plants phylogenetically related to the source decompose the substratum faster than fungi from unrelated sources that also differ in quality from the substratum	Fungi from the same or related sources (1 and 3 together) vs. fungi from unrelated leaves of different quality (4)	ANCOVA, linear contrasts: Pairwise comparisons using two-sided tests and family error rate of $P = 0.05$	Marginally significant, $P = 0.056$	Text
C. Relatedness hypothesis, from II. B: Fungi from the same plant species or family as the substratum decompose leaves faster than the corresponding substrata means	Fungi from the same or related sources (1 and 3, respectively) vs. modeled means	ANCOVA, linear contrasts: Pairwise comparisons using two-sided tests and family error rate of $P = 0.05$	Same species or genus, faster but NS Related species, significant, but slower, $P < 0.0001$	Table 5
D. Relatedness hypothesis, from II. B: Fungi from a different plant family and different quality than the substrate result in slower decomposition than the corresponding substrata means	Fungi from leaves unrelated to and differing in quality from the source (4) vs. modeled means	ANCOVA, linear contrasts: Pairwise comparisons using two-sided tests and family error rate of $P = 0.05$	Different family and quality, significant, faster, $P = 0.0215$	Table 5
E. Source hypothesis, from II. A: Fungi decompose their source substratum faster than fungi from a different substratum	Mean rates of decomposition by fungi from the same or a related source (1 and 3, together) vs. mean decomposition by fungi isolated from unrelated sources (2 and 4)	ANCOVA, linear contrast: Pairwise comparisons using two-sided test and family error $P = 0.05$	Marginally faster, $P = 0.0668$	Text
F. Quality hypothesis, from II. A: Fungi from leaves related to the substratum cause faster decomposition when source and substratum have similar than different quality	Mean rates of decomposition by fungi from the same or a related source of similar quality (1) vs. mean decomposition by fungi isolated from related sources differing in quality (3)	ANCOVA, linear contrast: Pairwise comparisons using two-sided test and family error $P = 0.05$	Significant, but slower when fungi are from the same species or genus than fungi from the same family, $P = 0.0330$	Table 6
G. Quality vs. relatedness, from II. A: Matching of fungal sources and substrata by relatedness is equivalent to matching by quality	Mean rates of decomposition by fungi from an unrelated source matched by quality to the substratum (2) vs. mean decomposition rates by fungi from related leaves of different quality (3)	ANCOVA, linear contrast: Pairwise comparisons using two-sided test and family error $P = 0.05$	Significant, matching by relatedness faster than matching by quality $P = 0.0401$	Table 6

Note: Roman numerals show linkages between main hypotheses and subsequent tests.
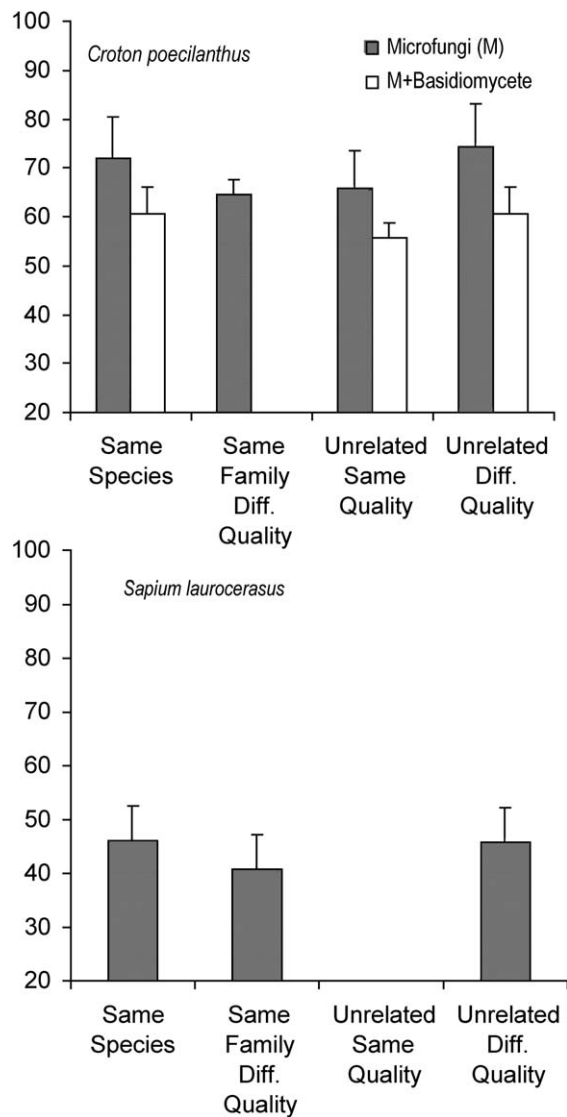
Figure 2. Percentage of mass remaining of three leaf species decomposed by microfungi in microcosms when the fungal source plant and substratum were matched by leaf quality and phylogenetic relatedness. Results are shown for *Croton poecilanthus* (a), and *Sapium laurocerasus* (b) although differences within plant species were only statistically significant for *C. poecilanthus*. Means for micrososms with *C. poecilanthus* leaves that had a basidiomycete contaminant in addition to the microfungal treatment are shown with open bars (a). Error bars represent one standard deviation.

were between the two fastest and two slowest decomposers of *S. lauroceraus*, CP1 and IV2 vs. IF1 and IV1 (Fig. 3d). All fungi that were from plants that were matched by relatedness to the *S. laurocerasus* substratum were in the fast group while all but one isolate from the completely mismatched fungus–substratum combinations were in the slow group.

Discussion

As summarized in Table 7, significant interactions and differences from modeled means were found in fungal source–substratum relationships. Matching dominant decomposer fungal substrata to their source leaves, either by plant phylogenetic relatedness or leaf quality, generally increased rates of decomposition as compared to mismatched sources and substrata, though matching by relatedness significantly increased rates of decomposition more often. Curiously, fungi from related leaves of different quality than the substratum decomposed leaves faster than when fungi were from the same leaf species as the substratum. The overall patterns, however, were consistent with the original hypothesis, and suggests that host recurrence among microfungal leaf decomposers may be significant for rates of decomposition in tropical forests.

Plants and decomposer communities have been proposed as interdependent subsystems, with each one carrying out processes mutually required for the long-term maintenance of the other (Mikola and Setälä, 1998a; Wardle, 1999, 2002; Naeem et al., 2000). Plants provide carbon and nutrients to detrital communities, which in turn control the release of mineral nutrients that are critical for maintaining plant productivity. Hooper et al. (2000) hypothesized that substrate 'selectivity' among decomposers and detritivores is normally distributed with most having intermediate levels of selectivity. Data from this and previous studies (Lodge, 1997) on occurrences and frequencies of leaf decomposer fungi among hosts in tropical forests are consistent with the Hooper et al. (2000) hypothesis.

We found large differences in microfungal species composition and rank dominance among decomposing leaf species, similar to previous results from tropical forests (Cowley, 1970; Cornejo et al., 1994; Polishook et al., 1996; Parungao et al., 2002). The mean percentage non-overlap among the 10 most frequent fungi cultured from five leaf species after 5 weeks decomposition was 68%, similar to levels of complementarity between two leaf species (68–74%) reported by Polishook et al. (1996) for all culturable microfungi from leaves in various states of decay. The most vegetatively dominant microfungus in *M. bidentata* leaves, *Pestilotiopsis* sp., was probably the same species as the first or second most frequent fungal isolate from decomposing *M. bidentata* leaves in the study by Polishook et al. (1996). While species overlap among dominant microfungi in this study was high between species from different plant families that
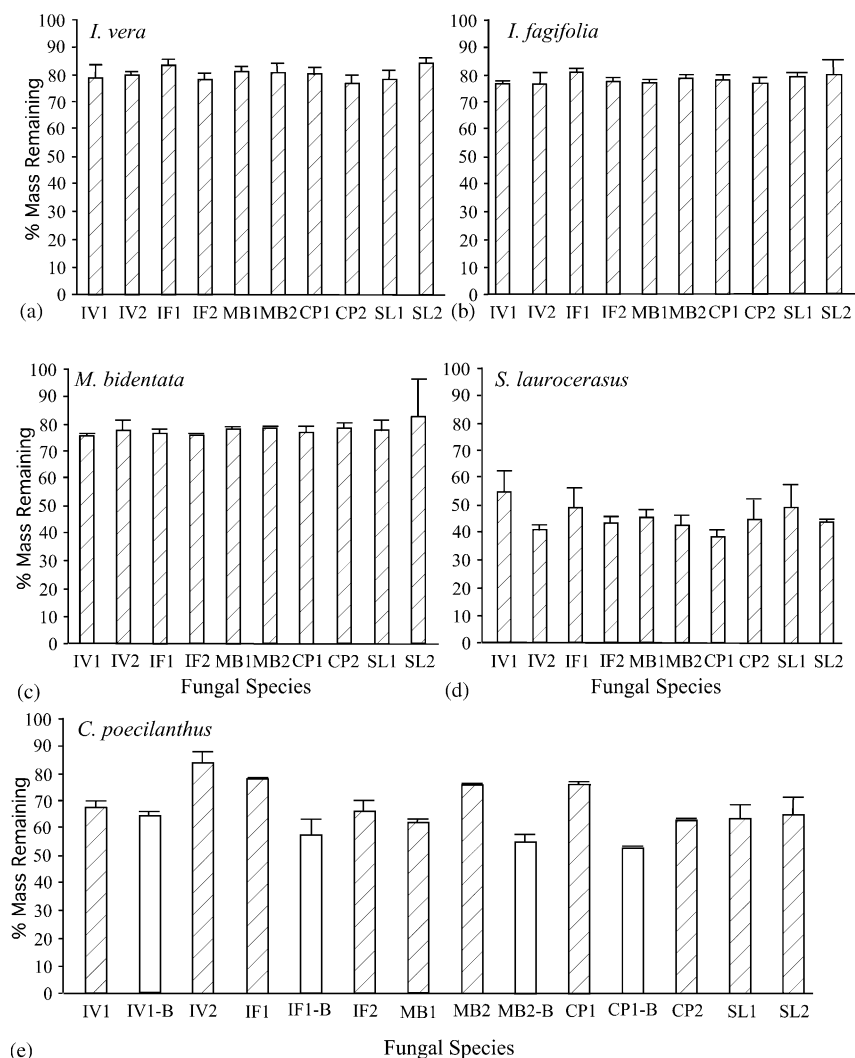
Figure 3. Mean percentage of mass remaining of five leaf species decomposed by individual species of microfungi in microcosms: *Inga vera* (a), *I. fagifolia* (b), *Manilkara bidentata* (c), *Sapium laurocerasus* (d) and *Croton poecilanthus* (e). Fungal codes begin with the first letters of the genus and species of their source leaf. Means for micrososms with *C. poecilanthus* leaves that had a basidiomycete contaminant in addition to the microfungal treatment are shown with open bars (e). Error bars represent one standard deviation.

were matched by quality, and between leaves of different qualities within the Euphorbiaceae, it was low between two *Inga* species that had similar quality. Spatial heterogeneity in microfungal communities may have contributed to differences in dominant microfungi between the *Inga* species. The *I. fagifolia* trees we used were in riparian areas while the *I. vera* trees were in uplands, so microenvironment may have differed between the two *Inga* species. Environmental differences have been found to greatly influence microfungal communities in tropical leaf litter (Cowley, 1970; Cornejo et al., 1994). Differences in microfungal communities within the same leaf species located

at spatially separated sites have been reported, but generally those differences were weaker than those found among different leaf species occurring together (Cowley, 1970; Polishook et al., 1996; Parungao et al., 2002). The degree of specialization among microfungi for particular plant families or substratum qualities may differ depending on plant groups. Our two species in the Euphorbiaceae, which shared half of their dominant species, had high concentrations of calcium in their leaves, an element that has been shown to promote certain microfungal species and influence fungal community composition (Christiansen, 1969; Widden, 1986).

Goubière and Corman (1987) suggested that fungal species that form functional decomposer assemblages are widespread but that assemblages might vary between forest systems. Evidence from some reciprocal leaf decomposition experiments have shown faster decomposition in leaf litter placed in the community of origin rather than in another plant community, suggesting that some detrital communities may be adapted to breaking down particular types of substrata. This pattern is referred as 'home-court advantage', and has been found for low-quality leaf litter in forest plantations in Brazil (De Asiss Olivereira et al., 1998) and for some temperate pine and aspen forests (Hunt et al., 1998; González et al., 2003). In our study, microfungal decomposers showed faster decomposition of their own substratum or substrata that were related or similar to their source leaves as compared to unrelated and dissimilar substrata. Our data are thus consistent with a home-court advantage, and support the contribution of early microfungal leaf decomposers to this phenomenon in tropical forests.

The reason why different fungi are recurrent (i.e., differentially abundant) on different hosts is unclear, and may involve leaf structure, leaf chemistry, or the fact that a few of the fungi present in decomposing leaves are endophytic in green leaves and persist as saprobes on the forest floor (Polishook et al., 1996). Fallen leaves from different plant species can differ greatly in their contents of lignin, cellulose, secondary plant compounds and other components; some may be inhibitory to fungal growth while each requires a diverse array of microbial enzymes for their degradation (Parkinson, 1981; Kjøller and Struwe, 1982; Heal and Dighton, 1986; Wainwright, 1988; Cromack and Caldwell, 1992; Cox et al., 2001). Such differences in leaf components may contribute to differences in microfungal species composition and frequencies (Bills and Polishook, 1994a; Polishook et al., 1996; Wong and Hyde, 2001; Zhou and Hyde, 2001) that have been documented among plant species and communities (Swift, 1976; Christiansen, 1981, 1989; Cook and Rayner, 1984), including both temperate (Christensen, 1969) and tropical forests (Cowley, 1970; Cornejo et al., 1994; Polishook et al., 1996; Lodge, 1997). In our study, e.g., *Xylaria* spp. were among the 10 most frequent early leaf decomposers in the four litter species that had moderate to high levels of lignin, but were absent from *S. laurocerasus* that had only 2.2% lignin. Osono and Takeda (2002) and Urairuj et al. (2003) noted that *Xylaria* species were exceptional among microfungal leaf decomposers in having ligninolytic enzymes. On the other

hand, Flanagan (1981), Kjøller and Struwe (1980, 1982, 1987), Wainwright (1988), Sin et al. (2002) and Bucher et al. (2004) found that most fungi were versatile in their carbon utilization, which is consistent with the hypothesis of Hooper et al. (2000). Nevertheless, diversity of carbon substrates would still be expected to increase decomposer diversity given intermediate levels of substrate selectivity among the decomposers (Hooper et al., 2000).

The role of host 'selectivity' and fungal diversity in controlling rates of decomposition and nutrient mineralization are unclear (Zak and Rabatin, 1997). Gochenaur (1981) found that decomposition rates were independent of microfungal rank abundance in their source leaves. In contrast, we found that the rate of decomposition was generally faster when dominant microfungi from source leaves were matched to substrata either by phylogenetic relatedness or quality of the source and substratum leaves as compared to mismatched source–substratum combinations. Fungi from the same species or one related to the substratum caused greater mass loss than fungal dominants from unrelated leaves with dissimilar quality. In comparisons among fungal dominants from leaves that were dissimilar in quality to the substratum, decomposition was faster with fungi from plants related than those unrelated to the substratum. The pattern of faster decomposition by fungi from plants related to the source plant but with a different quality than the substratum than by fungi from unrelated source plants with similar quality to the substratum is dubious, as there were no differences in weight loss among *C. poecilanthus* leaves decomposed by fungi that were matched to the substratum by species, family or quality when the two representative fungi from each leaf species were grouped (Fig. 2a).

We observed the highest decomposition rates in a few microcosms that had basidiomycete contaminants in addition to a microfungus. This result is probably best explained by the ligninolytic properties of basidiomycete fungi (Cromack and Caldwell, 1992; Osono and Takeda, 2002). Osono and Takeda (2002) and Urairuj et al. (2003) also found that basidiomycetes and species of *Xylaria* with ligninolytic capabilities caused the greatest mass loss. It is possible that the basidiomycete species allowed the microfungi to gain access to resources that were bound up with or protected by lignin. Thus, while the early decomposer microfungi were capable of decomposing leaves in the absence of other microbes, the effects of both microfungi and basidiomycetes was additive in at least some combinations. The microfungi and basidiomycetes thus represent different functional groups.

Positive correlations between decomposition and number of species in detrital food webs have been reported (Naeem et al., 2000) but it was not clear if those differences were attributable to greater numbers of functional groups (Morin, 2000). In contrast, Degens (1998) found no decrease in decomposition with a reduction in microbial functional groups, and Cox et al. (2001) found a decrease in the rate of early decomposition in the presence of multiple decomposer fungi. Robinson et al. (1993) found that combative interactions were energetically costly among fungal decomposers grown in mixtures on wheat straw, resulting in increases in the rate of CO_2 evolution, and potentially influencing rates of decomposition. Widden and Scatolin (1988) and Cox et al. (2001) suggested that fungal assemblages were patchily distributed depending on which species arrived first and how they competed with each other.

Our data on early stage microfungal decomposers suggest that 'selectivity' for related hosts, which contributes to species diversity of decomposer fungi in tropical forests, affects rates of decomposition (Table 7). Whether a disturbance or environmental stress would affect long-term rates of decomposition by reducing the diversity of decomposer fungi or causing shifts in decomposer community composition is less clear because of potential redundancies. The evidence for home-court advantage in some previous reciprocal leaf litter decomposition experiments in both temperate and tropical forests, however, suggest that there are at least short-term consequences for rate of decomposition associated with shifts in detrital communities.

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