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Biodiversity hanging by a thread: the importance of fungal litter-trapping systems in tropical rainforests

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The exceptionally high species richness of arthropods in tropical rainforests hinges on the complexity of the forest itself: that is, on features such as the high plant diversity, the layered nature of the canopy and the abundance and the diversity of epiphytes and litter. We here report on one important, but almost completely neglected, piece of this complex jigsaw—the intricate network of rhizomorph-forming fungi that ramify through the vegetation of the lower canopy and intercept falling leaf litter. We show that this litter-trapping network is abundant and intercepts substantial amounts of litter (257.3 kg ha^{-1}): this exceeds the amount of material recorded in any other rainforest litter-trapping system. Experimental removal of this fungal network resulted in a dramatic reduction in both the abundance (decreased by 70.2 $\pm$ 4.1%) and morphospecies richness (decreased by 57.4 $\pm$ 5.1%) of arthropods. Since the lower canopy levels can contain the highest densities of arthropods, the proportion of the rainforest fauna dependent on the fungal networks is likely to be substantial. Fungal litter-trapping systems are therefore a crucial component of habitat complexity, providing a vital resource that contributes significantly to rainforest biodiversity.

Keywords: arthropods; biodiversity; canopy; fungi; leaf litter; rainforest

1. INTRODUCTION

The mechanisms underlying the extraordinary diversity and distribution of arthropods in tropical rainforests are not fully understood [1], but are often attributed to the physical and biological complexity of the ecosystem. Accumulations of leaf litter in rainforest canopies provide an important living space for a diverse community of animals that would otherwise be confined to the forest floor [2–4]. This component of the forest ecosystem greatly enhances the range and extent of species interactions and ecosystem processes, such as nutrient dynamics and moisture retention that can occur within the canopy [5,6]. It is generally assumed that the vast majority of canopy litter accumulates in epiphytes, on large branches, and on specialized understory trees [7,8]. However, leaf litter can also be held by an assemblage of marasmioid fungi which form aerial rhizomorph networks that permeate the lower canopy of tropical rainforests [9,10].

The litter-trapping marasmioid fungi comprises *Marasmius* spp. (hence marasmioid) and a few antecedent members of that genus [10–12]. These fungi are well adapted to the variable moisture conditions of the forest canopy with marcescent basidiomata and tough persistent rhizomorphs [9,10]. The black and brown rhizomorphs, between 0.1 and 1.5 mm in diameter, form adhesion zones to living and dead material and create intricate networks, which intercept and anchor falling leaf litter creating stable, abundant litter-trapping deposits with a widespread distribution throughout moist tropical forest canopies [10] (figure 1*a*). Although we are certain that the litter-trapping fungi we are studying here are marasmioid fungi, their species identification is notoriously difficult since basidiomata are usually not found, and genetic distinctions between these fungi remain controversial [10,12], though a number of species have previously been identified [9,10].

We investigate here the hypothesis that this characteristic, but previously neglected, feature of the rainforest ecosystem might play an important role in the maintenance of canopy biodiversity. We quantify the effectiveness of these fungal networks in trapping litter and provide experimental evidence of their vital contribution to the abundance and diversity of arthropods living in the forest canopy.

2. METHODS

The study was conducted in lowland mixed dipterocarp forest in Danum Valley Conservation Area, Sabah, Malaysia (5°01′ N, 117°40′ E, altitude *ca* 170 m [14]). We surveyed the vertical and horizontal distribution of fungal litter-trapping systems and estimated the quantity of litter retained along ten 100 m transects (greater than 100 m apart). Every 10 m the number of isolated fungal systems [10] and dry mass of the fungal rhizomorphs and suspended litter were recorded within a 4 m^2 area to a height of 3 m. To assess whether fungal systems were distributed non-randomly, a χ^2 goodness-of-fit test was performed and the coefficient of dispersal (CD) was calculated. To determine the amount of leaf litter held by fungal systems below 3 m, we used a linear regression of fungal mass against litter mass to estimate the background level of suspended litter (as the intercept). This was then subtracted from each sample before calculating the mean leaf litter held in the fungi (see the electronic supplementary material).

The vertical distribution of fungal systems was evaluated in 25 m^2 areas, positioned every 20 m along the transects, with presence/absence of fungal systems recorded with a clinometer in cardinal directions at heights of 1, 5, 10, 15 and 20 m and maximum height. The total quantity of leaf litter held by the fungi throughout the canopy was estimated from the relationship between fungal occurrence and canopy height, which provided the proportion of fungal systems below 3 m. Assuming a linear relationship between the occurrence of fungal systems and the amount of litter held with height, we estimated the total suspended litter from the known mass of fungal-associated litter below 3 m (see the electronic supplementary material).

Arthropods were sampled from 60 paired sites (each site—4 m^2 and 3 m high). We removed the fungal network and associated leaf

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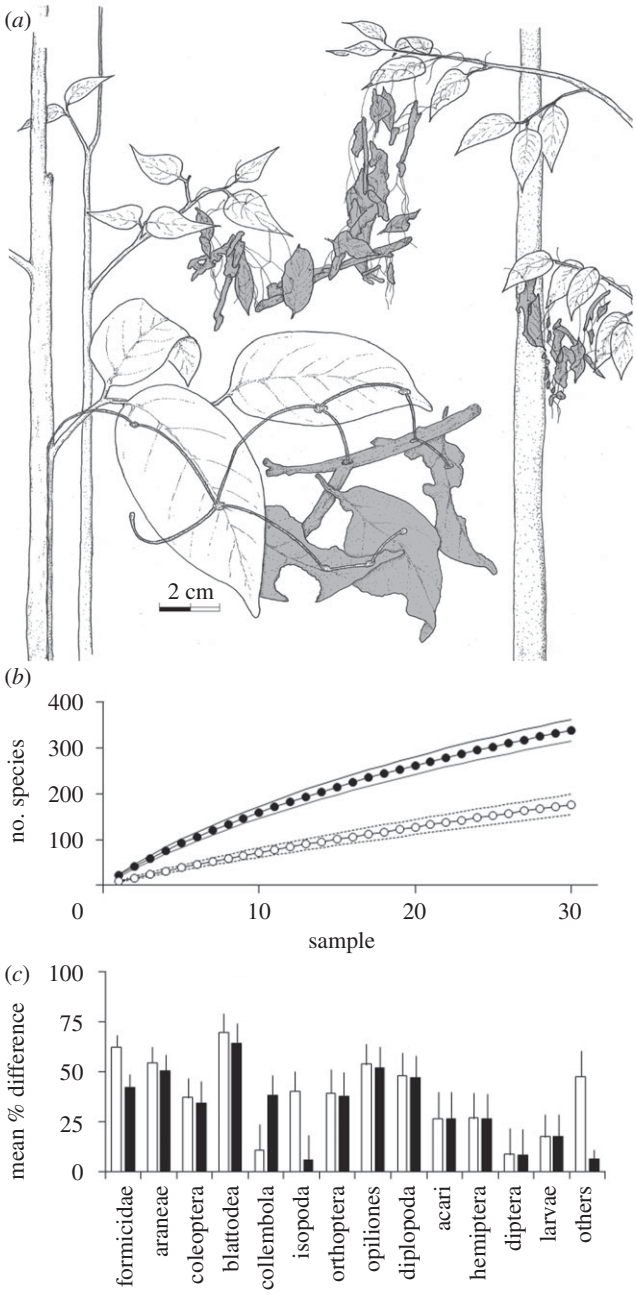

Figure 1. Differences between arthropod communities in the two treatments. (*a*) Litter-trapping fungal networks showing rhizomorph connections between intercepted leaf litter and the living vegetation. (*b*) Morphospecies accumulation curves plotted by sample (curves are the product of 50 randomizations, 95% confidence intervals shown) [13] filled circles, with fungal networks; unfilled circles, without fungal networks. (*c*) Mean percentage difference in abundance (unfilled bar) and morphospecies richness (filled bar) between samples with and without fungal networks for the different arthropod taxa (s.e. of the mean shown).

litter from one of each of the paired sites. In the control sites, the fungal network was left intact, but the disturbance simulated by thoroughly shaking the vegetation. After 10 days, re-established arthropod communities were sampled by fumigating the area with Ridsect and beating the vegetation and fungal networks. Arthropod specimens were identified to ordinal-level (order for hexapods and class for millipedes and centipedes) and classified to morphospecies [15] using digital images to compare morphological features (Moticam 2000 microscope camera).

Temperature and relative humidity were measured at each collection point using a LogIT data logger, and canopy cover was estimated using a spherical densiometer. Differences in richness and abundance were tested using linear models, which included environmental factors.

We compared the ordinal-level composition of arthropod assemblages collected with existing canopy and forest floor datasets from the same locations [16], using ordination techniques (detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA)). Canopy samples were collected by fogging with Pybuthrin 33BB non-persistent insecticide to a height of approximately 15 m (four 1 m^2 collection trays at each site, $n = 20$). Arthropods from forest floor litter samples (four 1 m^2 areas of leaf litter were collected at each site, $n = 20$) were extracted using Winkler-type apparatus [16]. Analyses were run using all four unpaired arthropod assemblage datasets, and then subsequently using only the datasets of the two paired fungal treatments. To assess turnover between communities, we calculated Sørenson's index and also a modified version that takes into account unsampled taxa for all the communities at the ordinal level and for fungal treatments at the morphospecies level [13].

In all analyses, site was included as a random factor, with the exception of the first set of ordinations. We identified the most parsimonious models on minimizing Akaike information criterion (AIC) for both univariate and multivariate analyses.

3. RESULTS

Fungal systems occurred in all transects, 85 per cent of sampling sites, and had a highly clumped distribution (d.f. = 4, $\chi^2 = 30.92$, $p < 0.001$; CD = 2.5). Fungi networks were observed up to a height of 47 m, although occurrence declined with height (see the electronic supplementary material). A mean dry weight of 56.7 ± 10.1 kg ha^{-1} of fungal-associated leaf litter was collected below 3 m. Based on this measurement and the decline in fungal occurrence with height; fungal systems hold 257.3 ± 45.8 kg ha^{-1} of dry weight litter.

In total, 1538 arthropods (339 morphospecies) were collected. Experimental removal of fungal networks and associated leaf litter caused reductions in arthropod abundance (9.8 ± 1.1 versus 41.4 ± 4.1 individuals per sample; decreased by $70.2\% \pm 4.1$; $F_{1,29} = 89.5$, $p = <0.001$, $n = 30$), and morphospecies richness (8.4 ± 0.9 versus 21.8 ± 1.5 morphospecies per sample; decreased by $57.4\% \pm 5.1$; $F_{1,26} = 89.2$, $p = <0.001$, $n = 30$; figure 1*b*), with declines evident across most taxa (figure 1*c*). Fungal network removal also resulted in a shift in arthropod ordinal-level composition (CCA: $F_{1,103} = 2.29$, $p = <0.001$), with communities becoming more similar to those from the rest of the canopy and less similar to those in ground litter, although still significantly different from both (CCA: canopy, $F_{1,102} = 16.0$, $p = <0.001$; leaf litter, $F_{1,102} = 43.3$, $p = <0.001$; figure 2). Levels of turnover were low for all comparisons (see the electronic supplementary material).

4. DISCUSSION

Fungal litter-trapping systems are a characteristic feature of many tropical rainforests, and have been documented in other tropical regions such as South America and Papua New Guinea [10]. We found them to be very abundant, although their distribution was highly clumped, probably owing to spatial variation in microclimate [17,18]. Our results show that the fungi intercept and hold leaf litter in substantial quantities, approximately 257.3 kg of leaf litter per hectare, which substantially exceeds that recorded from other rainforest litter-trapping systems, for example, epiphyte mats (88 kg ha^{-1}) [7] and bromeliads (100 kg ha^{-1}) [4]. It is therefore clear that

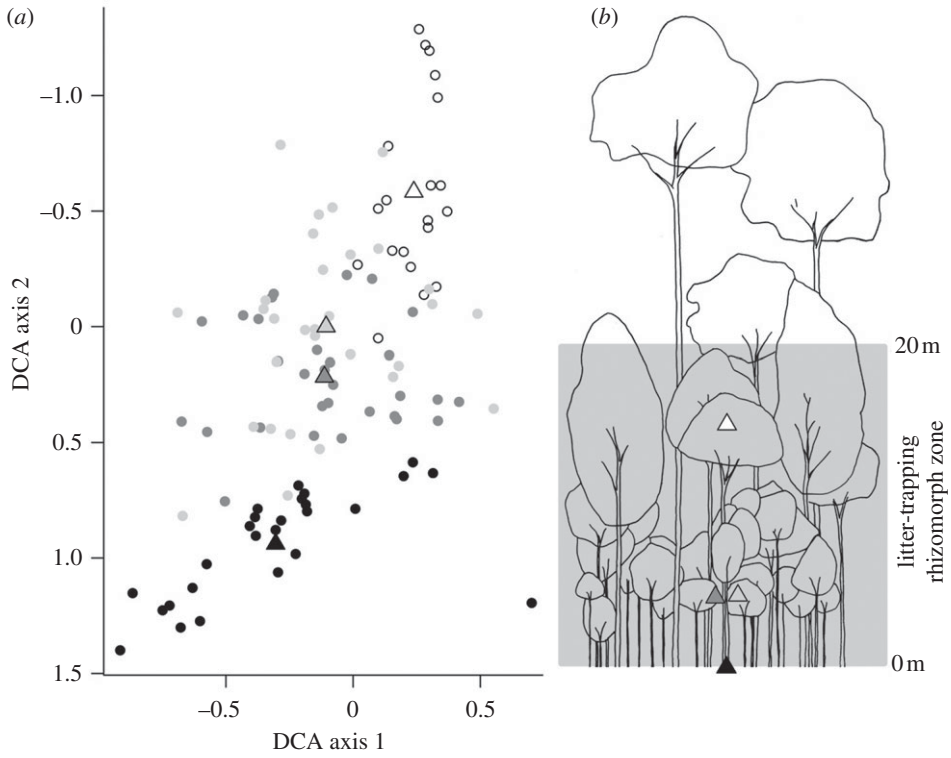

Figure 2. (*a*) Ordination plot (DCA) of ordinal-level arthropod assemblages collected from the canopy, forest floor and from plots with and without fungal networks. Centroids for the four arthropod assemblages are plotted as triangle symbols with different colours for each forest component. Unfilled circles, canopy; light grey circles, without fungal networks; dark grey circles, with fungal networks; filled circles, litter. (*b*) Sampling heights for each forest component plotted on a forest profile. The shaded area represents forest stratum in which of rhizomorph-forming litter-trapping fungi occur.

litter-trapping fungi provide potential living space and food for a wide variety of organisms and an extensive medium for a range of ecosystem processes. Owing to their abundance and distribution, fungal litter-trapping systems are likely to have a more distinct effect on canopy architecture than other canopy-litter accumulations and could provide a means of connection for arthropods living in more discrete habitats and links to the forest floor.

The removal experiment showed that approximately 70 per cent of arthropods in this lower canopy zone are supported by the fungal networks. This represents a considerable proportion of arthropods found in the forest canopy as a whole. Based on previous work [19] in the same forest, which showed that $60.7 \pm 5.1\%$ ($n = 6$) of arthropods were found in the lower 16 m of the canopy, approximately 43 per cent of canopy arthropods could therefore be dependent on these networks.

Although marasmioid fungal networks are widespread throughout the tropics [10], this is the first study to quantify their importance in trapping litter and providing a significant habitat for canopy arthropods. Fungal systems are known to be very sensitive to microclimatic changes [18] and it is clearly therefore vital to know the extent to which the marasmiozone can survive following habitat degradation and conversion to agricultural land, such as oil palm. Such losses may represent a previously un-catalogued element of tropical habitat change.

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