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Ecology and diversity of leaf litter fungi during early-stage decomposition in a seasonally dry tropical forest

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ARTICLE INFO

Article history:

Received 10 January 2015

Revision received 27 April 2015

Accepted 30 April 2015

Available online xxx

Corresponding editor:

Gareth W. Griffith

Keywords:

Dry tropical forest

Forest fire

Fungal diversity

Plant biomass

Saprotrophic fungi

ABSTRACT

Leaf litter samples of 12 dicotyledonous tree species (belonging to eight families) growing in a dry tropical forest and in early stages of decomposition were studied for the presence of litter fungi. Equal-sized segments of the leaves incubated in moist chambers were observed every day for 30 d for the presence of fungi. Invariably, the fungal assemblage on the litter of each tree species was dominated by a given fungal species. The diversity of fungi present in the litter varied with the tree species although many species of fungi occurred in the litter of all 12 species. A *Pestalotiopsis* species dominated the litter fungal assemblage of five trees and was common in the litter of all tree species. The present study and earlier studies from our lab indicate that fungi have evolved traits such as thermo-tolerant spores, ability to utilize toxic furaldehydes, ability to produce cell wall destructuring enzymes and an endophyte-litter fungus life style to survive and establish themselves in fire-prone forests such as the one studied here. This study shows that in the dry tropical forest, the leaf litter fungal assemblage is governed more by the environment than by the plant species.

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Introduction

Microbial communities play a major role in the decomposition of plant litter in terrestrial ecosystems. Fungi contribute substantially to this complex phenomenon of nutrient recycling in forest ecosystems as they elaborate an array of extracellular enzymes that deconstruct the different types of organic compounds in the litter (Baldrian and Lindahl 2011; Třifčáková et al. 2011) including lignocellulose which other organisms are unable to decompose (de Boer et al. 2005).

Studies on litter fungi of tropical ecosystems are limited compared to those in temperate ecosystems (Sayer 2006; McGuire et al. 2012; Xu et al. 2013). Many studies on litter fungi in the tropics pertain to fungi occurring in the litter of individual plant species such as *Maglielia garrettii* (Promputtha et al. 2002), *Magnolia liliifera* (Kodsueb et al. 2008), *Pandanus* sp. (Thongkantha et al. 2008), *Ficus* sp. (Wang et al. 2008), *Hevea brasiliensis* (Seephueak et al. 2010), *Anacardium occidentale* and *Pavetta indica* (Shanthi and Vittal 2010a, 2010b). Most of the studies from India on litter fungi are concerned with

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<http://dx.doi.org/10.1016/j.funeco.2015.05.004>

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identification of new fungal taxa or new reports for a region (Subramanian and Ramakrishnan 1953; Subramanian and Natarajan 1975; Subramanian and Sudha 1978; Subramanian and Bhat 1987; Subramanian 1992; D'Souza and Bhat 2002, 2013); very few investigations address the ecology of litter fungi (Sinsabaugh et al. 2002; Ananda and Sridhar 2004; Suryanarayanan et al. 2009). We designed a study to assess the diversity and distribution of litter fungi in a dry tropical forest by comparing the fungi occurring in the leaf litter of 12 different dicotyledonous tree species.

As the litter decomposes due to microbial activity, its chemical makeup is altered which in turn selects the species of microbes (including fungi) that are adapted to occupy this progressively decaying and dynamic substratum. This continues until decomposition is complete, and entails a succession of fungal species on litter which are arbitrarily classified as early, intermediate and late colonizers (Frankland 1998; Dickie et al. 2012). Hence, long-term monitoring is essential to determine changes in the fungal community during litter decomposition (Treseder et al. 2013). One-time samplings of litter for their fungal community have also been undertaken to answer various questions regarding their ecology (McGuire et al. 2012; D'Souza and Bhat 2013; Osono et al. 2013). In the present study we chose a one-time sampling method. Although this would not reveal the extent of contribution of different fungi to the complete decomposition of the litter, it helped to minimize the influence of environment on litter fungal community and facilitated comparison across tree species.

Materials and methods

Sample collection

Leaf litter samples of 12 tree species (belonging to eight families) from private lands located adjacent to the dry deciduous forest (DD) of the Mudumalai Wildlife Sanctuary (Lat. 11°32' and 11°43' N, Long. 76° 22' and 76° 45' E), which receives 1 200 mm of rainfall per annum were studied (Table 1). These were the most common tree species growing in this forest (Suryanarayanan et al. 2011a). DD constitutes the largest

expanse of Mudumalai Wildlife Sanctuary and experiences a continuous dry period from Nov. to Apr. Leaves are completely shed in Jan. and Feb. and new leaves are flushed by the end of Apr (Murali and Sukumar 1993). For each tree species, 20 mature, hard, brown leaves-representing neither freshly fallen nor in a state of advanced decay-from the floor of the forest (O horizon) were collected during Mar.–Apr. and processed as follows.

Isolation and identification of litter fungi

The moist chamber technique (Cannon and Sutton 2004) was used for isolating fungi from the leaf litter. Twenty fallen leaves were collected from the litter layer for each tree species (Table 1) and from each leaf five segments (approx. 0.5 cm²) were cut from the lamina region. The one hundred tissue segments thus obtained for each tree species were rinsed in sterile water. From these 100 segments, 90 were randomly selected and incubated in Petri dishes (9 cm dia) containing three layers of filter papers moistened with sterile water. Each Petri dish had nine tissue segments and the Petri dishes were sealed using Parafilm™ and incubated in a light chamber with a 12 hr light: 12 hr dark cycle at 26 ± 1 °C (Suryanarayanan 1992) for 30 d. The light chamber had a bank of three four foot Philips day light fluorescent lamps. The tissue segments received about 2 200 lux of light through the Petri dish lid. Three litter segments were observed under a microscope daily for the presence of fungal spores from 3 d of incubation onwards up to 30 d. The leaf litter segment was comminuted using sterile water and a scalpel, placed on a glass slide, stained with lactophenol and observed under a bright field microscope (×400, Nikon, Labophot 2) for the presence of fungal spores.

Fungi were identified based on their spore morphology and spore development. Every time a particular fungus was observed from a leaf segment, it was recorded as one isolate. The isolated fungi were identified using standard taxonomic keys (Ellis 1976; Subramanian 1971; Sutton 1980; Onions et al. 1981; Ellis and Ellis 1988; Nag Raj 1993; Hyde et al. 2000). Fungi that could not be identified were given codes (DLF 001, 002, 003, etc.) based on the size, shape, septation, ornamentation and pigmentation of the spores. Spores exhibiting similar morphology were grouped under one morphospecies (Arnold et al. 2000).

Detection of extracellular enzyme production by litter fungi

The method of Rohrmann and Molitoris (1992) and Kumaresan et al. (2002) were used for qualitative screening of the fungi for the production of amylase, cellulase, laccase, lipase, pectinase, pectate transeliminase, and protease enzymes. The methods involved growing the fungus in an agar medium amended with a suitable substrate and visually detecting the loss of substrate or the formation of the product due to enzyme action.

Statistical methods used

Percentage of Abundance (PA) (Van Ryckegem and Verbeken 2005) was given by:

Table 1 – Leaf litter of tree species studied for the presence of litter fungi

Tree species	Family	Code
<i>Anogeissus latifolia</i>	Combretaceae	AL
<i>Cassia fistula</i>	Caesalpiniaceae	CF
<i>Cordia wallichii</i>	Boraginaceae	CW
<i>Lagerstroemia microcarpa</i>	Lythraceae	LM
<i>Lagerstroemia parviflora</i>	Lythraceae	LP
<i>Ougeinia oojenensis</i>	Papilionaceae	OO
<i>Premna tomentosa</i>	Verbenaceae	PT
<i>Shorea roxburghii</i>	Dipterocarpaceae	SR
<i>Syzygium cumini</i>	Myrtaceae	SC
<i>Tectona grandis</i>	Verbenaceae	TG
<i>Terminalia bellerica</i>	Combretaceae	TA
<i>Vitexa litissima</i>	Verbenaceae	VA

$$PA \text{ of a taxon } A = \frac{\sum \text{records of taxon } A}{\sum \text{records of all taxa}} \times 100$$

Percentage of Occurrence (PO) (Van Ryckegem and Verbeke 2005) was given by:

$$PO \text{ of a taxon } A \text{ in a tree litter} = \frac{\sum \text{records of taxon } A}{\text{No. of leaf segments observed}} \times 100$$

The contribution to a litter fungal assemblage by the dominant fungi (DF) was calculated using the formula:

$$DF \text{ in a tree litter} = \frac{\sum \text{records of dominant taxon } A}{\sum \text{records of all taxa}} \times 100$$

Fisher's α was used for calculating the species diversity. It is calculated using the formula $S = a * \ln(1 + n/a)$, where S-number of taxa, n-number of individuals and a-the Fisher's alpha. This index was chosen as it is less affected by the abundance of common species (Magurran 2004). Biodiversity Pro version 2 (The National History Museum and The Scottish Association for Marine Science) and EstimateS software version 9.1.0 (Robert K. Colwell, University of Connecticut) [<http://viceroy.eeb.uconn.edu/estimates>] were the two statistical programs used for deriving various ecological parameters.

Jaccard's similarity index (JI) was calculated to compare the qualitative similarity between any two leaf species:

$$JI = \frac{c}{(a + b + c)} \times 100$$

where, a = number of fungal species in a leaf species, b = number of fungal species in another leaf species, c = number of fungal species common for both leaf species.

Results

In a 30 d incubation in moist chamber, the number of litter fungal species isolated from the litter segment of each tree species varied from 49 in *Lagerstroemia microcarpa* to 78 in *Ougeinia oojeinensis* and *Vitex altissima*; the number of isolates of litter fungi varied from 503 in *Terminalia bellerica* to 1371 in *O. oojeinensis* (Table 2). The maximum number of isolates was recovered from the litter of *O. oojeinensis*. The species diversity

of litter fungi was lowest for *T. bellerica* (Fisher's α 9.21) and maximum for *V. altissima* (19.5) (Table 2). Most of the fungal species isolated belonged to the Ascomycotina (the dominant ones belonging to Helotiales, Hypocreales, Microascales, Pleosporales and Xylariales) represented by both anamorphic and teleomorphic forms. The sufficiency of sampling of fungi which sporulated at the time of sampling was ascertained by plotting species accumulation and unique species curves (Fig 1A) as well as a singleton curve (Fig 1B) for the fungal species isolated in all the litter samples. The influence of sample sequence on the shape of the accumulation curve was avoided by randomizing the data 100 times using the computer software EstimateS for plotting the curve (Suryanarayanan et al. 2011a) (Fig 1). A 'J' shaped curve was obtained when the % abundance of the fungal species was plotted indicating that the assemblage at the time of observation was dominated by one or two fungal species only and the rest of the fungal species were less abundant. A representation of this trend, which was seen in the litter of all the tree species studied here, is given in Fig 2. While different fungi dominated the fungal assemblage in the litter of different tree species, a *Pestalotiopsis* sp. dominated the assemblage in the litter of *Cassia fistula*, *L. microcarpa*, *Syzygium cumini*, *T. bellerica* and *V. altissima* (Table 3).

Its % occurrence and % dominance in the litter ranged from 58.9 to 97.8 and 7.1 to 17.5 respectively (Table 3). Furthermore, in the litter of seven of the tree species (*Anogeissus latifolia*, *Cordia wallichii*, *L. parviflora*, *O. oojeinensis*, *Premna tomentosa*, *Shorea roxburghii* and *Tectona grandis*) where this fungus was not dominant, its % occurrence was 50 and above. The % abundance of fungi such as *Cladosporium cladosporioides*, *Colletotrichum* sp. 1, *Corynespora cassicola*, *Idriella lunata*, *Nigrospora oryzae*, *Periconia* sp., *Pestalotiopsis* sp. and *Spegazzinia parkeri* was relatively higher in the litter of many tree species.

To understand the litter community composition better, the data accumulated from the 30 d observation for all the tree species were split into three groups of 10 d each and analyzed further. This revealed that the total number of species and isolates as well as the species diversity recovered from the decaying leaf samples increased initially and started to fall later (Table 4). *Pestalotiopsis* sp. dominated the overall litter assemblage throughout the 30 d incubation; *Colletotrichum* sp. 1 was co-dominant during the early period and *Periconia* sp. was dominant during the later period. To discern any pattern in the frequency of distribution of litter fungi, the data ranged were further analysed by considering only those morpho-species which appeared in the litter samples of six or more tree species. This showed that fungi such as *Alternaria alternata*, *Arthrinium* sp., *Colletotrichum* sp. 1, *Lasiodiplodia theobromae*, *Nectria* sp., *N. oryzae*, *Periconia* sp., *Pestalotiopsis* sp., *Phoma* sp. and *Wiesneriomyces javanicus* occurred in the litter of all 12 tree species and were present throughout the study period. *Cercospora* sp., *C. cassicola*, *Curvularia lunata*, *Drechslera australiensis*, *Glomerella* sp., and *Sporidesmium* sp. were also very prevalent and could be recovered from the litter of 11 tree species. Of the 47 morphospecies (which appeared in the litter of six or more plant species), 42 were isolated from *V. altissima* while only 30 were isolated from the litter sample of *S. roxburghii* and *T. bellerica*. The presence of a few fungal species such as *Chaetomium* sp., *Periconia* sp., and *Zygosporium* sp.

Table 2 – Comparison of species diversity of litter fungi in the leaf litter of 12 tree species. Data represent total of 30 d observation

Tree species	No. of isolates	No. of species	Fisher's α
<i>Anogeissus latifolia</i>	698	59	15.4
<i>Cassia fistula</i>	732	56	14.1
<i>Cordia wallichii</i>	1 141	69	16.2
<i>Lagerstroemia microcarpa</i>	656	49	12.3
<i>Lagerstroemia parviflora</i>	613	60	16.5
<i>Ougeinia oojeinensis</i>	1 371	78	17.9
<i>Premna tomentosa</i>	884	71	18.2
<i>Shorea roxburghii</i>	696	57	14.7
<i>Syzygium cumini</i>	611	54	14.3
<i>Tectona grandis</i>	979	73	18.3
<i>Terminalia bellerica</i>	503	37	9.21
<i>Vitex altissima</i>	1 054	78	19.5

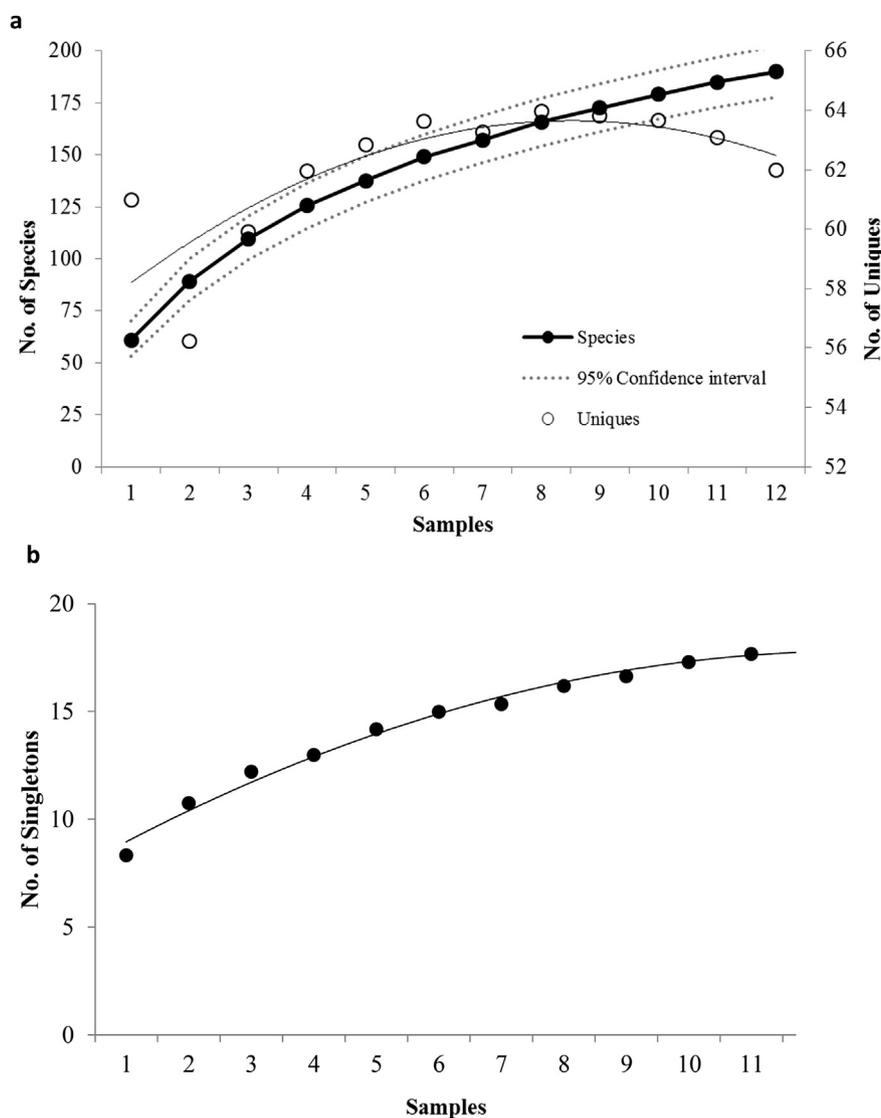


Fig 1 – (A) Species accumulation and number of unique species curves for litter fungi isolated from twelve different tree species of dry deciduous forest. Data were randomized 100 times for plotting the graph. The uniques curve represents a polynomial trend line. (B) Number of singletons for litter fungi isolated from twelve different tree species of dry deciduous forest. The singletons curve represents a polynomial trend line.

increased with incubation time while a reverse trend was seen for a few other species including *Cercospora* sp., *C. clado-sporioides*, *Colletotrichum* spp., *Corynespora* sp., *D. australiensis*, and *Fusarium* sp. A comparison of the rarefaction curves showed that the litter of *O. oojeinensis* supported more fungal species for a given number of isolates while that of *T. bellerica* supported the least number of species (Fig 3). A Jaccard's similarity index showed that the overlap of fungal species occurring on the leaf litter of the 12 tree species ranged from 25.11 % (between SR and AL) to 67.46 % (between SC and CF) (Table 5).

Forty six fungi isolated from the different litters were screened by agar plate assays for the production of extracellular enzymes. More than 80 % of them were positive for lipase and cellulase. Pectinase was produced by 78 % of the fungi tested; 65 % of them produced pectate transeliminase, 63 % produced protease enzymes and 59 % produced amylase

(Fig 4). A *Phoma* sp. isolated from the litter of *Radermachera xylocarpa* and a *Robillarda* sp. from the litter of *O. oojeinensis*, *R. xylocarpa* and *T. grandis* produced all the enzymes tested.

Pestalotiopsis sp. isolated from *R. xylocarpa* litter elaborated all the enzymes except amylase.

Discussion

Plant biomass represents a complex mixture of rapidly degradable and recalcitrant nutrient sources for the biomass decomposing fungi. Hence, a succession of fungi is observed during litter decay represented by those saprotrophic species adapted to utilize the different types of nutrients present in it. Each stage in the succession could alter the nutrient status and the chemistry of the substratum leading to the creation of a different niche which would then be colonized by another

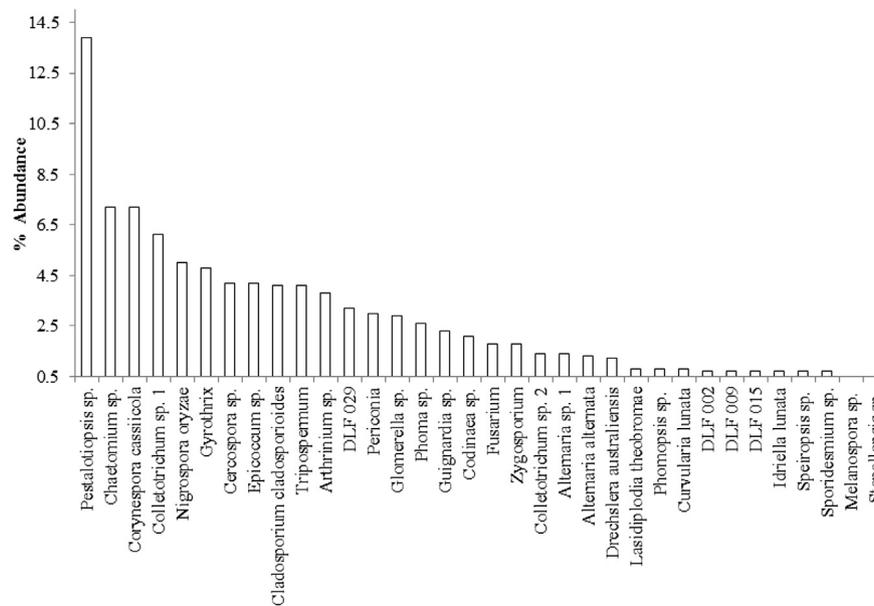


Fig 2 – Percentage abundance of fungi in the litter of *S. cumini* after 30 d incubation.

set of fungal species. This dynamic nature of decomposition necessitates continuous and long-term monitoring of plant litter to record the complete succession and species diversity of litter fungi (Voříšková and Baldrian 2013). While long-term studies are needed for understanding the dynamics of litter decay and estimating the diversity of the fungi involved in the process (Sayer 2006; Treseder et al. 2013), studying a given successional phase is important as it reveals the key species involved and their diversity in the sequential alteration of biomass. It is with this aim that we studied the leaf litter of 12 tree species of the DD forest in the early stage of decomposition. It should be stressed that the litter samples were visually graded as in their early state of decomposition and their exact stage of decay was not known; this and the fact that the difference expected in the chemistry of the leaves of the 12 different tree species could be the reason for the

difference in the number of species contained in a given number of fungal isolates as exemplified by the rarefaction curves (Fig 3). For quantifying diversity, it is imperative that the sampling method used is effective in capturing as many species as possible. The flattening of the species accumulation curve and the falling of the unique species curve (Fig 1A) indicated that our sampling was adequate and nearly complete at least for the fungi which could sporulate on these substrata (Longino 2000; Henderson 2003; Suryanarayanan et al. 2011a). Furthermore, a plot of the singletons also showed that the appearance of singletons progressively decreased with increase in sample size (Fig 1B); this could also be taken as an indication that the asymptote of species accumulation curve is nearing. It is likely that this might change when a molecular approach is made to account even for the non-sporulating forms. The difference in the number of isolates and species diversity of the fungi observed on the litter of different trees (Table 2, Fig 3) could be attributed to the difference in the texture, ratio of lignin:cellulose and secondary metabolites content in the litter (Berg and McLaugherty 2003; Voříšková et al. 2011; Talbot and Treseder 2012). A

Table 3 – Percentage of occurrence and % abundance of dominant fungi in the leaf litter of tree species

Tree code	Dominant fungus	% Occurrence	% Abundance
AL	<i>Idriella lunata</i>	92.2	11.9
CF	<i>Pestalotiopsis</i> sp.	71.1	8.7
CW	<i>Spegazzinia parkeri</i>	91.1	7.2
LM	<i>Pestalotiopsis</i> sp.	58.9	8.1
LP	<i>Subulispota</i> sp.	67.8	10.0
OO	<i>Periconia</i> sp.	94.4	6.2
PT	<i>Corynespora cassiicola</i>	93.3	9.5
SR	<i>Helminthosporium</i> sp.	74.4	9.6
SC	<i>Pestalotiopsis</i> sp.	93.3	13.7
TG	<i>Nectria</i> sp.	50.0	4.6
TB	<i>Pestalotiopsis</i> sp.	97.8	17.5
VA	<i>Pestalotiopsis</i> sp.	83.3	7.1

Table 4 – Species diversity, number of isolates and species, and dominant fungi in leaf litter of 12 tree species after 10, 20 and 30 d of incubation

	10 d	20 d	30 d
Total no. of isolates	3 638	3 900	2 400
Total no. of species	158	165	136
Fisher's alpha (α)	33.7	34.9	31.3
Dominant species	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis</i> sp.
Co-dominant species	<i>Colletotrichum</i> sp. 1	<i>Periconia</i> sp.	<i>Periconia</i> sp.

phylogenetic factor may be affecting the occurrence of litter fungi at this stage of decomposition since the Jaccard similarity index was almost 40 for LP and LM in the same genus and 55 % for PT and TG belonging to the same family (Table 5). However, the overlap of species composition on all the litter was high (25–67 %) showing that there were many generalists capable of exploiting the different litter in this forest, thereby suggesting the stronger role of environment in determining the fungal assemblage on the litter (Table 5). Fungi such as *C. cladosporioides*, *I. lunata*, *Pestalotiopsis* sp. and *Xylaria* sp., which are reported to be abundant in the leaf litter of wet tropical forests (Polishook et al. 1996; Santana et al. 2005), were also dominant or commonly isolated in the litter we studied.

Similarly, the species abundance distribution of the fungi also followed the known pattern of a few abundant and many rare species (Polishook et al. 1996) (Fig 2). In all litter types, fungi belonging to the Ascomycota were predominant (Table 3). Culture-based and molecular studies have confirmed that ascomycetes invariably dominate the litter of most plants in early stages of decay (Frankland 1998; Santamaría and Bayman 2005; Aneja et al. 2006; Jumpponen and Jones 2009; Poll et al. 2010; Seephueak et al. 2010).

Extracellular enzymes of litter microbes directly determine their community organization and litter composition (Sinsabaugh et al. 2002). According to Sinsabaugh et al. (2002), plant biomass degradation by microbes follows a successional

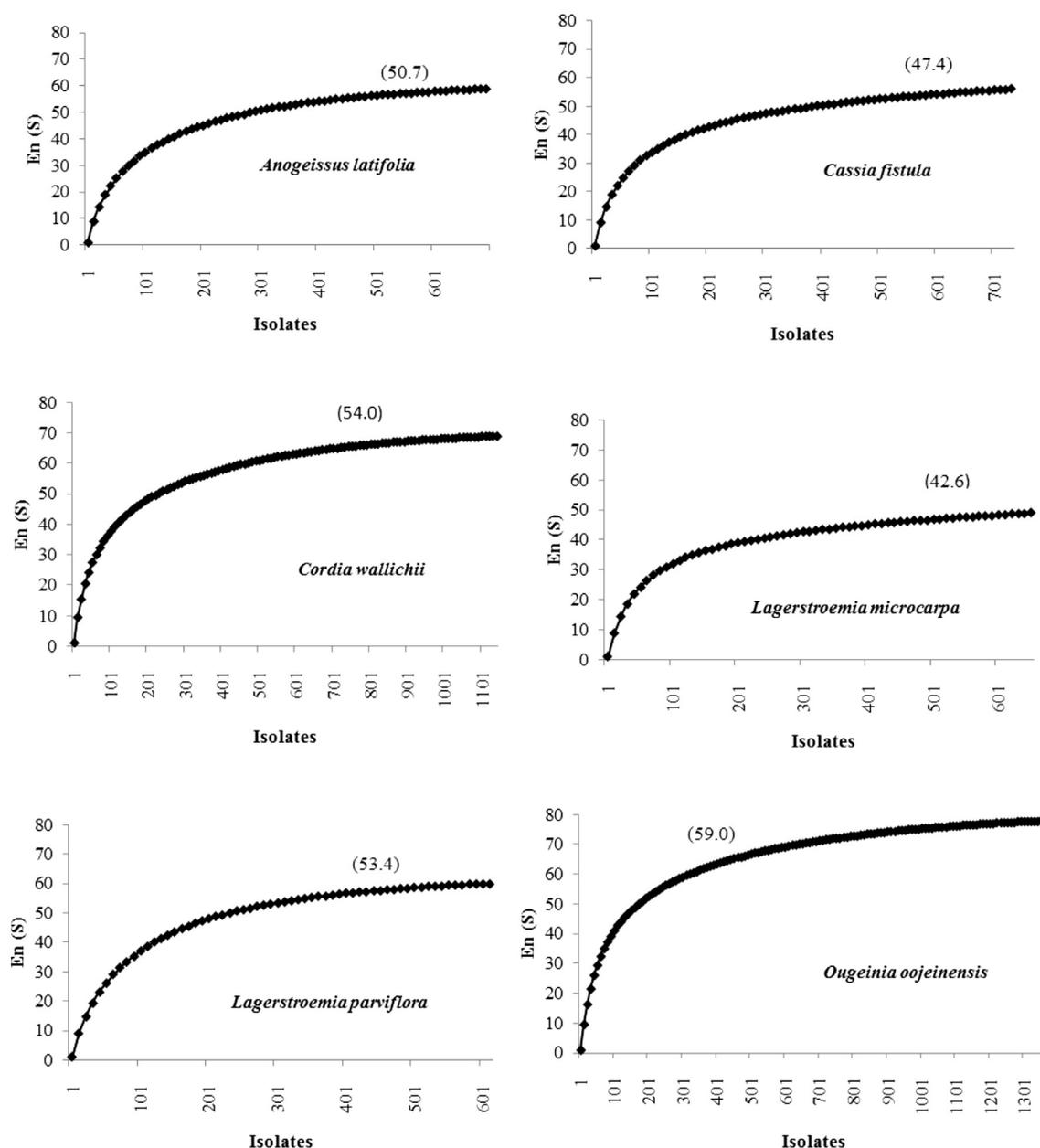


Fig 3 – Rarefaction curves for the expected number of species [En(S)] of litter fungi from leaf litter of 12 different tree hosts in dry tropical forest. Number in parenthesis indicated the number of species expected to be present in 301 isolates of fungi.

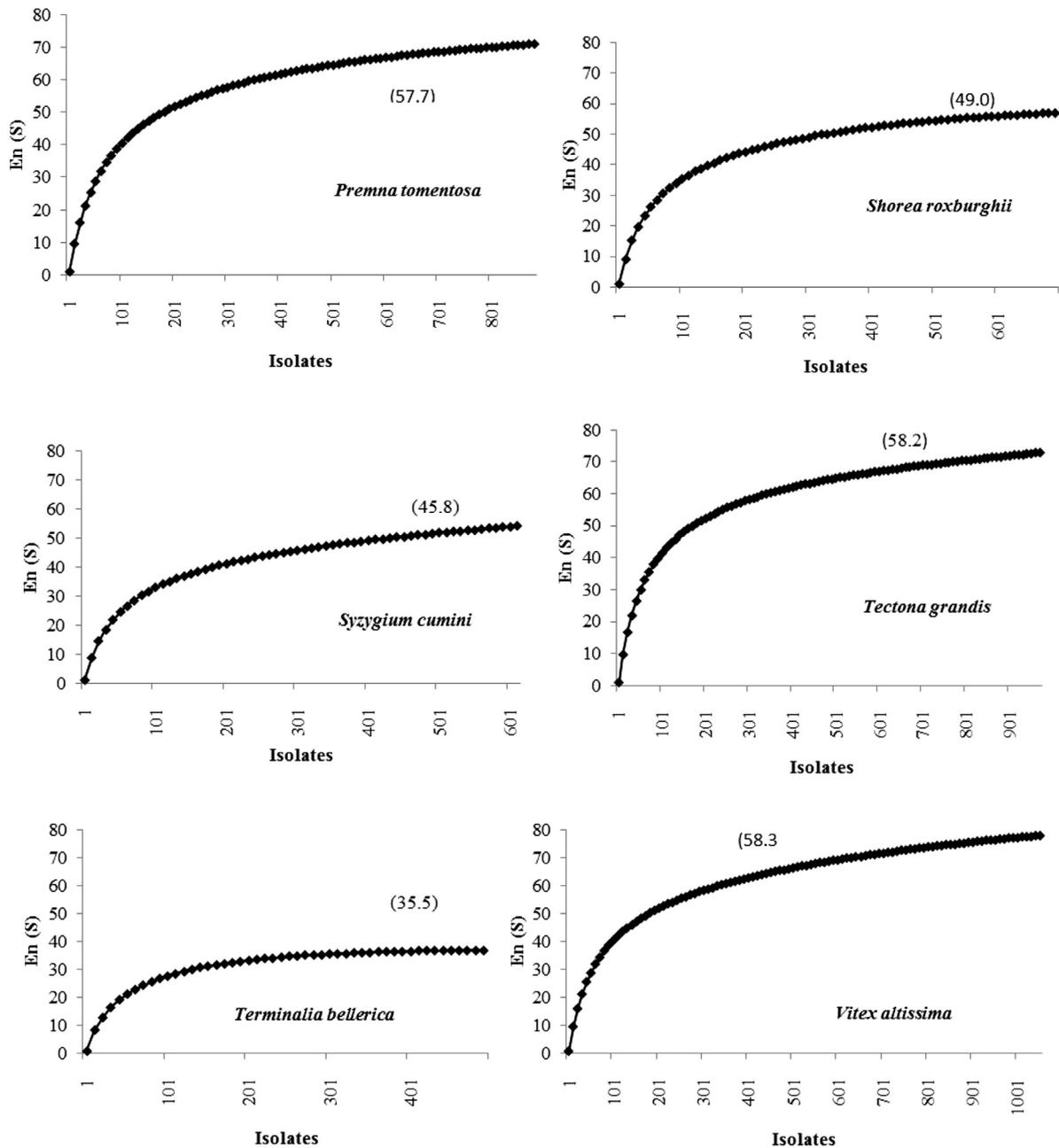


Fig 3 – (continued)

loop where the substratum selects the microbial community, which elaborates extracellular enzymes that deconstruct and modify the existing substratum, and this modified substratum then selects a suitable microbial community thus ensuing microbial succession. Consistent with the observation that cellulose decomposition ability is common among saprotrophic ascomycetes (Weber et al. 2011), we found that most of the fungi tested produced cellulases (Fig 4). We also observed that 50 % of the isolates screened for extracellular enzymes produced laccases which play a role in lignin decomposition. Although basidiomycetes are the major decomposers of lignin in the litter and appear at a later stage in the succession (Osono 2007), some saprotrophic ascomycetes also produce extracellular lignolytic enzymes thus contributing to lignin

decomposition (Liers et al. 2006). Although basidiomycetes generally colonize the litter during relatively advanced stages of decomposition, when lignin would be the major residual carbon source (Frankland 1998), the absence of these fungi in our study could be attributed to the following reasons as well. It is possible that the small size of the litter fragments used could have precluded these fungi (Lodge et al. 2008). A more likely explanation is that this forest experiences a prolonged seasonal dry period and the samples were collected during the dry period; unlike in the wet tropical forests where basidiomycete colonization of even the newly fallen leaves through pre-existing rhizomorphs and hyphal cords is favoured by moisture, the moisture limitation in our forest site could have prevented litter colonization by these fungi (Lodge et al. 2014).

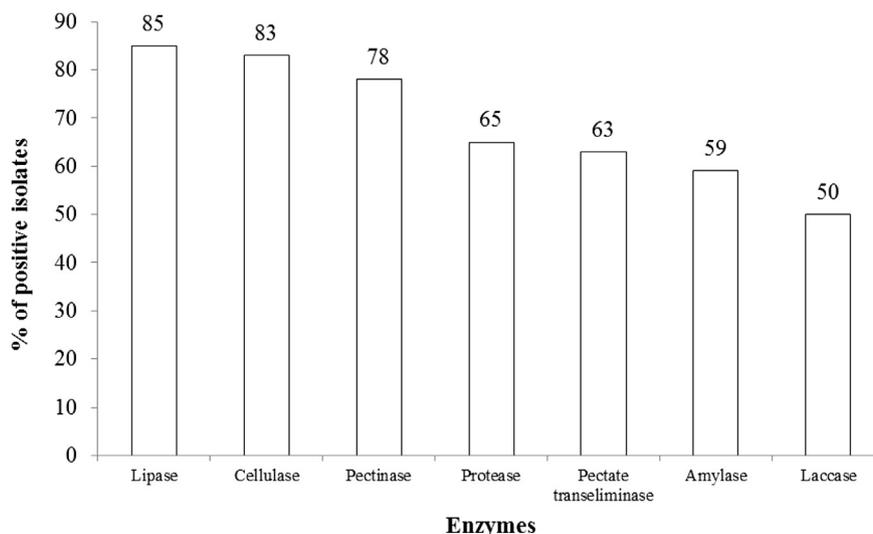
Table 5 – Jaccard Similarity index for fungi isolated from the leaf litter of 12 different tree species

	AL	CF	CW	LM	LP	OO	PT	SR	SC	TG	TB	VA
AL		32.87	29.69	34.86	38.14	31.13	28.57	25.11	33.31	29.82	37.64	29.34
CF			36.63	43.52	48.77	29.96	46.78	45.52	67.46	43.37	46.15	44.46
CW				36.17	31.81	35.75	39.11	30.38	33.33	40.75	28.59	40.27
LM					39.56	38.48	37.53	32.25	39.78	39.27	37.10	40.12
LP						26.41	34.60	46.29	51.31	32.16	46.06	34.43
OO							36.36	26.80	29.06	44.68	26.89	42.23
PT								42.66	41.61	55.18	32.16	51.08
SR									45.60	34.51	31.36	39.09
SC										39.25	57.99	44.44
TG											41.57	59.22
TB												45.73
VA												

Generally, the early stage leaf litter is rapidly colonized by many fungal species with no species dominating the assemblage (Seephueak et al. 2010). As the litter ages and is altered by the action of these pioneer fungi, new species begin to colonize the litter resulting in increased diversity (Voříšková and Baldrian 2013). We also observed this trend as the diversity of fungi increased on the 20th d compared to that on the 10th d of incubation (Table 4). Being an *in vitro* study, however, this is also likely due to the difference in the time required for the different fungi to sporulate on the litter substratum.

It is increasingly recognized that molecular and next generation sequencing approaches provide more complete estimates of litter fungal diversity than traditional culture-based investigation such as the one used in the present study (Voříšková and Baldrian 2013). However, a culture based study could help in understanding the functional basis of fungal presence in the litter as described below. Here, our results are in consonance with that of Xu et al. (2013) who state that the plant species as a factor does not influence greatly the composition of litter fungal community. In the present study, a *Pestalotiopsis* sp. appeared to be a more successful litter fungus

as it was (i) present in the litter in all tree species belonging to taxonomically disparate families, (ii) dominant in the litter of many of the tree species (Fig 2 and Table 3), and (iii) dominated the overall fungal assemblage for the 30 d study (Table 4). This ecological fitness of this fungus could be attributed to the following. The DD forest is a seasonally dry tropical forest experiencing prolonged dry periods and periodic forest fires during the dry seasons (Mondal and Sukumar 2014). Suryanarayanan et al. (2011b) reported that the conidia of a *Pestalotiopsis* sp. occurring in the litter of these fire-prone forests are heat tolerant and survive exposure to 105 °C for 5 hr. Furthermore, this fungus utilizes furaldehydes, the most abundant volatile compounds formed during biomass burning (which are toxic to most fungi), as a source of carbon and also produces cellulase enzyme (Govinda Rajulu et al. 2014). These adaptations along with the ability of the genus to produce many of the biomass destructuring enzymes (present study) could ensure its dominant and constant presence in the litter of different trees species [representing different resources (Cornwell et al. 2008)]. Murali et al. (2007) reported that *Pestalotiopsis* spp. survive as foliar endophytes in many tree species

**Fig 4 – Percentage of litter fungi producing different extracellular enzymes (agar plate assay n = 46).**

of the dry deciduous forest currently studied for the litter fungal diversity. Earlier works have suggested that foliar endophytes could persist in leaf litter and switch to a saprotrophic mode of life style and function as pioneer litter decomposers (Kumaresan and Suryanarayanan 2002; Korkama-Rajala et al. 2008; Voříšková and Baldrian 2013). Notwithstanding the fact that a molecular approach is needed to establish if the *Pestalotiopsis* species exhibiting all the above traits and existing in these dry topical forests belong to one or different species, it appears that, as a genus, *Pestalotiopsis* is well adapted to exploit successfully the ecological niche as an early/mid stage litter decomposer. This line of argument could be extended to the more prevalent litter fungal genera occurring in the litter of different tree species in the present study such as *Alternaria*, *Chaetomium*, *Drechslera* and *Fusarium*, *Bartalinia* and *Curvularia* as these fungi utilize furaldehydes as carbon source (Govinda Rajulu et al. 2014); interestingly, the last two fungi also produce thermotolerant spores (Suryanarayanan et al. 2011b).

Our results suggest that in the relatively dry tropical forests, environment plays a greater role compared to the tree species in determining the assemblage of saprotrophic fungi in the litter at least during the early stage of decomposition. Circumstantial evidence suggests that fungi with specific traits selected by the environment could evolve into generalists occupying both living tissues (endophytes) and dead tissues (litter fungi) of a wide variety of plants thus depressing the overall fungal diversity in these ecosystems (Govinda Rajulu et al. 2014).

Acknowledgements

We thank Prof. R. Sukumar, Indian Institute of Science, Bangalore, for the help in the collection of leaf litter samples and the Secretary, Ramakrishna Mission Vidyapith, Mylapore, Chennai for providing facilities. TSS acknowledges the financial assistance by Ministry of Environment and Forests (23/36/03-RE), Government of India, New Delhi. We thank Prof. Felix Baerlocher, Department of Biology, Mount Allison University, Canada and the two anonymous referees for critically reading the manuscript and for their valuable suggestions.

REFERENCES

- Ananda, K., Sridhar, K.R., 2004. Diversity of filamentous fungi on decomposing leaf and woody litter of mangrove forests in the southwest coast of India. *Current Science* 87, 1431–1437.
- Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C., Schloter, M., 2006. Microbial colonization of beech and spruce litter-influence of decomposition site and plant litter species on the diversity of microbial community. *Microbial Ecology* 52, 127–135.
- Arnold, A.E., Maynard, Z., Gilbert, G.S., Coley, P.D., Kursar, T.A., 2000. Are tropical fungal endophytes hyperdiverse? *Ecology Letters* 3, 267–274.
- Baldrian, P., Lindahal, B., 2011. Decomposition in forest ecosystems: after decades of research still novel findings. *Fungal Ecology* 4, 359–361.
- Berg, B., McClaugherty, C., 2003. *Plant Litter: decomposition, humus formation, carbon sequestration*. Springer, Berlin.
- Cannon, P.F., Sutton, B.C., 2004. Microfungi on wood and plant debris. In: Mueller, G.M., Bills, G.F., Foster, M.S. (Eds.), *Biodiversity of Fungi Inventory and Monitoring Methods*. Elsevier Academic Press, Burlington, Mass, pp. 217–239.
- Colwell, R.K., 2013. Estimate S: Statistical Estimation of Species Richness and Shared Species from Samples. Version 9. Persistent URL <purl.oclc.org/estimates>.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Queded, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11, 1065–1071.
- de Boer, W., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews* 29, 795–811.
- Dickie, I.A., Fukami, T., Wilkie, J.P., Allen, R.B., Buchanan, P.K., 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecological Letters* 15, 133–141.
- D'Souza, M.A., Bhat, D.J., 2002. *Didymobotryum spirillum*, a new synnematous hyphomycete from India. *Mycologia* 94, 535–538.
- D'Souza, M.A., Bhat, D.J., 2013. Occurrence of microfungi as litter colonizers and endophytes in varied plant species from the Western Ghats forests, Goa, India. *Mycosphere* 4, 567–582.
- Ellis, M.B., 1976. *More Dematiaceous Hyphomycetes*. Surrey, U.K, CMI, Kew.
- Ellis, M.B., Ellis, J.P., 1988. *Microfungi on Miscellaneous Substrates: an identification handbook*. Croom Helm Ltd., London, U.K.
- Frankland, J.C., 1998. Fungal succession: unraveling the unpredictable. *Mycological Research* 102, 1–15.
- Govinda rajulu, M.B., Lai, L.B., Murali, T.S., Gopalan, V., Suryanarayanan, T.S., 2014. Several fungi from fire-prone forests of southern India can utilize furaldehydes. *Mycological Progress* 13, 1049–1056.
- Henderson, P.A., 2003. *Practical Methods in Ecology*, third edn. Blackwell Science Ltd, Oxford.
- Hyde, K.D., Taylor, J.E., Fröhlich, J., 2000. *Genera of Ascomycetes from Palm*. Fungal Diversity Press, Hong Kong.
- Jumpponen, A., Jones, K.L., 2009. Massively parallel 454 sequencing indicates hyperdiverse fungal communities in temperate *Quercus macrocarpa* phyllosphere. *New Phytologist* 184, 438–448.
- Kodsueb, R., Mckenzie, E.H.C., Lumyong, S., Hyde, K.D., 2008. Fungal succession on woody litter of *Magnolia liliifera* (Magnoliaceae). *Fungal Diversity* 30, 55–72.
- Korkama-Rajala, T., Müller, M.M., Pennanen, T., 2008. Decomposition and fungi of needle litter from slow- and fast-growing Norway spruce. *Microbial Ecology* 56, 76–89.
- Kumaresan, V., Suryanarayanan, T.S., 2002. Endophyte assemblages in young, mature and senescent leaves of *Rhizophora apiculata*: evidence for the role of endophytes in mangrove litter degradation. *Fungal Diversity* 9, 81–91.
- Kumaresan, V., Suryanarayanan, T.S., Johnson, J.A., 2002. Ecology of mangrove endophytes. In: Hyde, K.D. (Ed.), *Fungi of Marine Environments*. Fungal Diversity Research Series, vol. 9. Fungal Diversity Press, Hong Kong, pp. 145–166.
- Liers, C., Ullrich, R., Steffen, K.T., Hatakka, A., Hofrichter, M., 2006. Mineralization of ¹⁴C-labelled synthetic lignin and extracellular enzyme activities of the wood-colonizing ascomycetes *Xylaria hypoxylon* and *Xylaria polymorpha*. *Applied Microbiology and Biotechnology* 69, 573–579.

- Lodge, D.J., McDowell, W.H., Macy, J., Ward, S.K., Leisso, R., Claudio Campos, K., Kuhnert, K., 2008. Distribution and role of mat-forming saprobic basidiomycetes in a tropical forest. In: Boddy, L., Frankland, J.C. (Eds.), *Ecology of Saprobian Basidiomycetes*. Academic Press, Elsevier LTD., Amsterdam, pp. 195–208.
- Lodge, D.J., Cantrell, S.A., González, G., 2014. Effects of canopy opening and debris deposition on fungal connectivity, phosphorus movement between litter cohorts and mass loss. *Forest Ecology and Management* 332, 11–21.
- Longino, J.T., 2000. What to do with the data. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (Eds.), *Ants Standard Methods for Measuring and Monitoring Biodiversity*. Smithsonian Institution Press, Washington, pp. 186–203.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell science ltd, U.K.
- McGuire, K.L., Fierer, N., Bateman, C., Treseder, K.K., Turner, B.L., 2012. Fungal community composition in neotropical rain forests: the influence of tree diversity and precipitation. *Microbial Ecology* 63, 804–812.
- Mondal, N., Sukumar, R., 2014. Characterising weather patterns associated with fire in a seasonally dry tropical forest in southern India. *International Journal of Wildland Fire* 23, 196–201.
- Murali, K.S., Sukumar, R., 1993. Leaf flushing and herbivory in a tropical deciduous forest, southern India. *Oecologia* 94, 114–119.
- Murali, T.S., Suryanarayanan, T.S., Venkatesan, G., 2007. Fungal endophyte communities in two tropical forests of southern India: diversity and host affiliation. *Mycological Progress* 6, 191–199.
- Nag Raj, T.R., 1993. *Coelomycetous Anamorphs with Appendage-bearing Conidia*. Mycologue Publications, Ontario, Canada.
- Onions, A.H.S., Allsopp, D., Eggins, H.O.W., 1981. *Smith's Introduction to Industrial Mycology*, seventh ed. Edward Arnold, London, U.K.
- Osono, T., 2007. Ecology of ligninolytic fungi associated with leaf litter decomposition. *Ecological Research* 22, 955–974.
- Osono, T., Tateno, O., Masuya, H., 2013. Diversity and ubiquity of xylariaceous endophytes in live and dead leaves of temperate forest trees. *Mycoscience* 54, 54–61.
- Polishook, J.D., Bills, G.F., Lodge, D.J., 1996. Microfungi from decaying leaves of two rain forest trees in Puerto Rico. *Microbial Diversity* 17, 284–294.
- Poll, C., Brune, T., Begerow, D., Kandeler, E., 2010. Small-scale diversity and succession of fungi in the detritusphere of rye residues. *Microbial Ecology* 59, 130–140.
- Promptutha, I., Lumyong, S., Lumyong, P., McKenzie, E.H.C., Hyde, K.D., 2002. Fungal succession on senescent leaves of *Manglietia garrettii* in Doi Suthep-Pui National Park, northern Thailand. *Fungal Diversity* 10, 89–100.
- Rohrmann, S., Molitoris, H.P., 1992. Screening for wood-degrading enzymes in marine fungi. *Canadian Journal of Botany* 70, 2116–2123.
- Santamaria, J., Bayman, P., 2005. Fungal epiphytes and endophytes of coffee leaves (*Coffea arabica*). *Microbial Ecology* 50, 1–8.
- Santana, M.E., Lodge, D.L., Lebow, P., 2005. Relationship of host recurrence in fungi to rates of tropical leaf decomposition. *Pedobiologia* 49, 549–564.
- Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews of the Cambridge Philosophical Society* 81, 1–31.
- Seepheueak, P., Petcharat, V., Phongpaichit, S., 2010. Fungi associated with leaf litter of para rubber (*Hevea brasiliensis*). *Mycology: An International Journal of Fungal Biology* 1, 213–227.
- Shanthi, S., Vittal, B.P.R., 2010a. Fungi associated with decomposing leaf litter of cashew (*Anacardium occidentale*). *Mycology: An International Journal on Fungal Biology* 1, 121–129.
- Shanthi, S., Vittal, B.P.R., 2010b. Biodiversity of microfungi associated with litter of *Pavetta indica*. *Mycosphere* 1, 23–37.
- Sinsabaugh, R.L., Carreiro, M.M., Repert, D.A., 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. *Biogeochemistry* 60, 1–24.
- Subramanian, C.V., 1971. *Hyphomycetes: an account of Indian species, except Cercosporae*. ICAR, New Delhi, India.
- Subramanian, C.V., 1992. *Basauxia and Ashtaangam of Hyphomycetes from Southeast Asia*. *Korean Journal of Mycology* 20, 281–284.
- Subramanian, C.V., Bhat, D.J., 1987. Hyphomycetes from south India I. some new taxa. *Kavaka* 15, 41–74.
- Subramanian, C.V., Natarajan, K., 1975. Two new Hyphomycetes from India. *Mycologia* 67, 1211–1217.
- Subramanian, C.V., Ramakrishnan, K., 1953. *Pligionema*, A new genus of the Sphaeropsidales. *The Journal of the Indian Botanical Society* 32, 131–136.
- Subramanian, C.V., Sudha, K., 1978. *Ardhachandra*, a new genus of the Hyphomycetes. *Canadian Journal of Botany* 56, 729–731.
- Suryanarayanan, T.S., 1992. Light-incubation: a neglected procedure in mycology. *The Mycologist* 6, 144.
- Suryanarayanan, T.S., Thirumalai, E., Prakash, C.P., Govindarajulu, M.B., Thirunavukkarasu, N., 2009. Fungi from two forests of southern India: a comparative study of endophytes, phellophytes and leaf litter fungi. *Canadian Journal of Microbiology* 55, 419–426.
- Suryanarayanan, T.S., Murali, T.S., Thirunavukkarasu, N., Govinda Rajulu, M.B., Venkatesan, G., Sukumar, R., 2011a. Endophytic fungal communities in woody perennials of three tropical forest types of the Western Ghats, southern India. *Biodiversity and Conservation* 20, 913–928.
- Suryanarayanan, T.S., Govinda Rajulu, M.B., Thirumalai, E., Reddy, M.S., Money, N.P., 2011b. Agni's fungi: heat-resistant spores from the Western Ghats, southern India. *Fungal Biology* 115, 833–838.
- Sutton, B.C., 1980. *The Coelomycetes. Fungi Imperfecti with Pycnidia, Acervuli and Stromata*. CMI, Kew, Surrey, U.K.
- Talbot, J.M., Treseder, K.K., 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry–decay relationships. *Ecology* 93, 345–354.
- Thongkantha, S., Lumyong, S., McKenzie, E.H.C., Hyde, K.D., 2008. Fungal saprobes and pathogens occurrence on tissues of *Dracaena loureiri* and *Pandanus* spp. *Fungal Diversity* 30, 149–179.
- Ťifčáková, L., Dobiášová, P., Kolářová, Z., Koukol, O., Baldrian, P., 2011. Enzyme activities of fungi associated with *Picea abies* needles. *Fungal Ecology* 4, 427–436.
- Treseder, K.K., Bent, E., Borneman, J., McGuire, K.L., 2013. Shifts in fungal communities during decomposition of boreal forest litter. *Fungal Ecology* 10, 58–69.
- Van Ryckegem, G., Verbeken, A., 2005. Fungal ecology and succession on *Phragmites australis* in a brackish tidal marsh. I. Leaf sheaths. *Fungal Diversity* 19, 157–187.
- Voříšková, J., Baldrian, P., 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. *ISME Journal* 7, 477–486.
- Voříšková, J., Dobiášová, P., Šnajdr, J., Vaněk, D., Cajthaml, T., Santrůčková, H., Petr Baldrian, P., 2011. Chemical composition of litter affects the growth and enzyme production by the saprotrophic basidiomycete *Hypholoma fasciculare*. *Fungal Ecology* 4, 417–426.
- Wang, H.-K., Hyde, K.D., Soyong, K., Lin, F., 2008. Fungal diversity on fallen leaves of *Ficus* in northern Thailand. *Journal of Zhejiang University SCIENCE B* 9, 835–841.
- Weber, C.F., Zak, D.R., Hungate, B.A., Jackson, R.B., Vilgalys, R., Evans, R.D., Schadt, C.W., Megonigal, J.P., Kuske, C.R., 2011. Responses of soil cellulolytic fungal communities to elevated

-
- atmospheric CO₂ are complex and variable across five ecosystems. *Environmental Microbiology* 13, 2778–2793.
- Xu, W., Shi, L., Chan, O., Li, J., Casper, P., Zou, X., 2013. Assessing the effect of litter species on the dynamic of bacterial and fungal communities during leaf decomposition in microcosm by molecular techniques. *PLoS ONE* 8 (12), e84613. <http://dx.doi.org/10.1371/journal.pone.0084613>.