

Review

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Review

Leaf-Litter Saprobes and Their Host Preference

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Abstract: Saprotrophism is a life mode exhibited by microfungi. Saprobes are cosmopolitan and occur in various habitats and ecological niches dwelling on diverse substrates and this contributes to the high numbers of fungi. Being abundant in litter, soil and decaying matter, they play crucial roles specifically towards mediating carbon and nutrient fluxes. Saprobic fungi in forest ecosystems may be host-specific or have host preferences and revealing this phenomenon will provide insights towards predicting global fungal numbers. In recent years, elucidation of saprobic fungi has been revolutionized through advances in molecular phylogenetics and the availability of genomic data, particularly in the Asean region. High-throughput sequencing and metagenomic approaches have revealed that the mycota are more diverse than previously established in samples in tropical forest ecosystems. This review discusses the role of fungi as saprobes, their host-specificity and host preference, their importance in litter decomposition and nutrient recycling, and their global dispersal. Approaches to establish fungal prevalence in the current genomic era are also discussed.

Keywords: forest saprobes; fungal diversity; high-throughput sequencing; leaf litter; recurrence

1. Leaf Litter

Leaf litter comprises the natural layer of fallen, senescent, dry, partially flat, or folded leaves accumulated on the ground under trees [1–3]. In tropical forests, leaf litter accounts for 70% of litter resulting in a total litterfall of up to 1.53 thousand kg/ha/yr [4], while 30% is contributed through twigs, seeds, flowers and other woody debris [5]. Litter is the leading and quickest deposited source of organic matter [6], and leaf litter contains substantial nutrients essential for fungal growth. In tropical forests, most of the nutrient stock is biomass, and relatively little is present in the soil [2]. Nutrients available in the plant litter that falls during the dry season are rapidly mineralized in the following monsoon and taken up by roots in the wet season. In contrast, forest floor litter is an integral part of the ecosystem, adding nutrients to form the humus layer in the soil [7], thereby enhancing soil productivity. Leaf litter likewise enters stream ecosystems, being subjected to microbial decomposition and physical leaching adding available nutrients to the streams [8–11].

Considering the different types of litter, broadleaf litter, which contains higher nutrients and lower levels of lignin and polyphenols in contrast to conifers leaf litter [12–15], undergoes rapid decomposition rates and mass loss due to higher content of soluble and leachable compounds. Due to this, broadleaf forests tend to have a rich litter forest floor inhabited by macro and microfauna [12,14,15]. In the soil, litter has multiple functions, such as a barrier to soil erosion, preventing soil aggregate destruction due to heavy rainfall, microclimate fluctuations, and soil compaction protection [16]. The litter layer provides nesting and shelter for organisms such as birds and small

animals [17–19]. Rainwater is filtered into the ground via the leaf litter layer, whereas litter decomposition is essential for nourishing the soil [1,16,18,20–22].

Microorganisms play a vital role in terrestrial ecosystems, acting as the major decomposers of plant litter [23]. Among them, fungal saprobes are instrumental in breaking down the organic compounds in plant litter, trapping the released elements in the fungal bodies, and preventing the elements from leaching [24–26], thereby supporting nutrient recycling and maintaining balance within forest ecosystems [27–29]. Leaf litter contains various nutrients; therefore, different fungal niches are colonized [30]. Litter fungi grow on substrates until they are completely decomposed. This entails a succession of fungal species throughout the decomposition process as early intermediate and late colonizers [31,32], dynamically changing their fungal community. This creates considerable diversity within the litter fungi, exhibiting high variations within the fungal community [30,33]. Consequently, elucidating the leaf litter dwelling saprobes unravels the hidden fungal diversity and builds up sexual-asexual relationships, providing insights to their ecological function in forest ecosystems.

2. Factors Affecting the Leaf Litter Decomposition Process

Many factors are responsible for the litter decomposition process. Among them, exogenous factors such as altitudinal gradient, temperature, and/or precipitation, nutrient availability, and endogenous factors such as leaf litter chemistry, nutrient content and secondary metabolites were reported to affect subsequent decomposition and mineralization [34–37]. Considering the fungal-mediated decomposition, for example, the rainy season facilitates a supportive environment for many leaf-litter inhabiting fungal mycelia to grow through highly porous, succulent, and moist leaf-litter layers [2,38,39], thereby increasing enzyme activity and fungal biomass. These conditions contribute to high litter decomposition rates in the wet season compared to the dry season, and leaf litter being the most significant part of the overall litter, provides a major contribution to converting into high biomass [40–44]. Further, the importance of humidity and suitable temperature regimes towards higher litter decomposition rates was discussed by [40,45]. Additional proof was provided by [46] that high-temperature regimes supported faster decomposition of holo-cellulose and lignin compared to low-temperature levels [47–52]. Given the provided facts, [53] further stated that the ability of saprobes to decompose leaf litter is more significant in warmer compared to cooler climates. These statements and results suggest that climatic variations considerably affect the litter decomposition process as well as the fungal-mediated litter decomposition.

Considering the endogenous factors, plant secondary metabolites and phenolic compounds are important in affecting leaf-litter decomposition by reducing and inhibiting microbial colonization [54–56]. The nutrient content of leaf litter, such as high levels of C and N, supports the increase in microbial colonization and subsequent decomposition rates, determining the fungal communities dominating during each stage of the decomposition process [57–60]. Leaf litter chemistry has more effect on variable compositions of fungal communities dominating different litter types [26,30]. On similar enzyme profiles, fungal communities harboured in two litter types of *Quercus petraea* were found to be distinct [26]. Consequently, this research evidence was able to validate the initial findings of [61] that different litter traits such as leaf toughness, nitrogen, lignin and polyphenol concentrations control the differential decomposition rates in leaf litter. Correspondingly, endogenous factors influence the differential dominance of fungal communities occupying a particular type of leaf litter influencing the decomposition process.

3. Role of Saprobes in Leaf Litter Decomposition and Nutrient Recycling

Leaf litter is a dynamic substratum where different stages of fungal colonization can be observed until its complete decomposition [31,32]. Throughout the decomposition period, the leaf litter composition alters, facilitating different groups of saprobic fungi to occupy and degrade different litter substrates, entailing succession [3]. These fungal communities are identified as early, intermediate, and late colonizers due to their progressive involvement in the complete decomposition of leaf litter [31,32].

Leaf litter succession increases fungal species richness and has been confirmed through molecular identification studies[62]. Factors such as decomposition stage, type of litter, moisture content, and substrate size were reported to affect the community and structure of leaf litter fungi [63,64]. Accordingly, fresh litter harbours a lower number of fungi. In contrast, a wide range of fungi were observed on half-decomposed litter and subsequently fewer fungi on well-decomposed litter [30,65]. Coelomycetes are vital in litter decomposition, and their population tends to decrease with increased decomposition [2]. Further insight into fungal succession was provided by [30]. In the early stages of decomposition, foliicolous epiphytes such as *Appendiculella* sp., *Ceramothyrium longivolcaniforme*, *Longihyalospora ampeli*, *Meliola* spp., *Micropeltis fici*, *M. ficinae*, *Mycoleptodiscus alishanense*, *Neophyllachora fici*, and *Zeloasperisporiales* sp. were found to be dominant. Despite being fewer in number, these species continued to colonize on the litter substrates. As the decomposition process moved into the intermediate stages, a diverse and higher number of saprobic Ascomycetes were reported. These included *Alternaria pseudoeichhorniae*, *Arthrinium sacchari*, *Hermatomyces biconisporus*, *Leptospora macarangae*, *Neodictyosporium macarangae*, *Nigrospora macarangae*, *Parawiesneriomyces chiayiense*, and *Periconia alishanica*. Towards the final stages of decomposition, the number of species reduced, with *Cladosporium* spp., *Penicillium* sp., and *Stachybotrys aloeticola* as dominantly reported taxa. These observations were made from the decomposition of *Macaranga tanarius* leaf litter [30]. Many asexual fungi were observed to be in higher frequencies during later stages of decay [66] mainly due to their competitive tolerance on litter substrates, which was also evident in the study[30].

Apart from the most recent study, studies conducted by [67] and [33] were found to be significant. Leaf litter succession on *Ficus pleurocarpa* observed similar trends with four noticeable colonization stages of saprobes while more similar taxa were abundant in advanced stages of decay. Species recorded in freshly fallen leaves were *Colletotrichum* sp., *Gaeumannomyces* sp., *Meliola* sp., *Pestalotiopsis* sp., *Phomopsis* sp., *Zygosporium echinosporum* and *Z. mansonii* followed by late colonizers such as *Volutella ramkurii*, *Selenodriella fertilis*, *Phomopsis* sp., *Ophiognomonia elasticae*, *Lanceispora amphibia*, and *Discomycete* sp. on leaf litter attributed to advanced decay. Fungal succession on leaf litter of *Manglietia garrettii* elucidated three successional communities reporting *Volutella* sp. as early colonizers, *Bionectria ochroleuca*, *Cylindrocladium floridanum*, *Dactylaria longidentata*, *Gliocladium* sp., *Hyponectria manglietiae* and *Lasiosphaeria* sp. as intermediate colonizers with a decline of species numbers with *Hyponectria manglietiae* and *Sporidesmium crassissporum* as late colonizers completing the decomposition [67].

Fungi are considered the main contributors to decomposing leaf litter due to their significant potential to reduce organic matter [56,68–70] by secreting a wide range of extracellular enzymes [60,71–74] including lignocellulose [75]. Most significant enzymes produced by leaf litter-dwelling saprobes, including *Alternaria*, *Aspergillus*, *Chaetomium*, *Fusarium*, *Myrothecium*, and *Penicillium* support the degradation of cellulases and hemicellulases, while *Arthrobotrys*, *Cephalosporium*, *Clavaria*, *Collybia*, *Fusarium*, *Verticillium*, *Absidia*, *Thamnidium*, and *Trichoderma* assist towards the degradation of lignin, chitin, and pectinases [69,76–79]. Phenol oxidases, peroxidases and laccases help catalyze lignin degradation [80], further disintegrating leaf litter. As aforementioned, different communities of fungi can be observed on each stage of litter decay, suggesting scope towards the discovery of obscure fungal taxa yet observing a more common assortment of fungal genera specifically dominating on leaf litter.

4. Host-Specificity, -Recurrence and -Preference

Host-preference, host-recurrence, and host-specificity were found to be standard terms associated among mycologists describing the differential abundance or, more often, the occurrence of microfungi in a particular host in comparison to the surrounding hosts [58,81–83]. Multiple studies have reported mycorrhizal fungi, plant pathogenic and endophytic life modes, and saprobic fungal taxa with affinity towards certain host species [84,85]. The underlying reason for a fungus to exhibit host-preference towards a particular host may be due to several factors [30,83,86].

Focusing on the leaves, foliar structure and chemical composition, leaf surface characteristics (waxes, hairy structures), thickness and toughness, phenolic compounds and secondary metabolites will preferentially act for fungal attachment and successful colonization [83,87–89]. The presence of endophytic fungi on living leaves, which supports initial decomposition during senescence, will subsequently have an influential effect towards fungal host-preference [90–94]. Several studies have been conducted building supporting evidence towards fungal host-preference and host-specificity focusing on succession and diversity on various hosts [67,86,87,95–98].

Multiple theories and hypotheses have been built up based on evidence from leaf litter fungi and their host-preference [67,83,87,95,96]. Stroma of *Pemphidium nypicolum* developed throughout the senescence of *Nypa* palm, transitioning from endophytic to saprobic life mode was reported by [99]. Many of the saprobes occurring on dead leaves and petioles of palms (*Astrosphaeriella*, *Myelosperma*, *Oxydothis*) have also been isolated as endophytes [48,100,101]. Endophytic fungi thrive on living leaves and persist as saprobes during senescence was suggested by [102]. Studies have stated that endophytic and saprobic taxa reported from these studies are the same species [103,104]. A discussion detailed by [90] has shown that most fungi have endophytic life stages and become saprobes or even pathogens when the leaves die, or the plant is stressed.

Preferential specificity of saprobes towards certain host species has been observed in tropical forest ecosystems by [95], stating many of the reported *Beltrania rhombica*, *Chaetospermum artocarpi*, *Dictyochaeta* sp., *Dictyosporium zeylanicum*, *Ellisiopsis galleisiae*, *Gliocladium cylindrospermum*, *Lanceispora* sp., *Lophodermum* sp. and *Ophioceras fusiforme* taxa happens to be unique to a single host. Host species such as *Agathis australis*, *Eucalyptus globulus*, *Nypa fruticans*, grasses, sedges and rushes, *Pandanus furcatus* and host genera including *Agathis*, *Metrosideros*, *Nothofagus*, *Eucalyptus* and palms such as *Arenga*, *Livistona*, *Oraniopsis*, *Oncosperma* and *Salacca* are reported to harbour multiple fungal taxa [75,99,105–118]. Saprobian fungi show specificity towards leaf or tissue types. For instance, *Dermataceae* taxa are found on the petioles and midribs of identified *Ficus* hosts [87]. Similarly, fruiting bodies of *Gnomonia queenslandica* have been observed on the petioles and midribs of *Elaeocarpus angustifolius* [116]. Preferential occurrence of fungi on leaves, rachis-tips, mid-rachides, and rachis-bases of palms were reported by [117]. Additionally, [118] noted a unique composition of fungal taxa on the senescent flowerheads of *Protea*. A possible reason for saprobe and tissue preferences can be the adaptation to tissues with latex and phenolic compounds acting as hostile environments for decomposer taxa [87]. Dominant groups of fungi in each host can be phylogenetically related to host species, preferring physical structure or chemistry in different leaf types, building a source and substratum relationship as suggested by [89].

Tropical rainforests harbour a diversity of plants, producing higher levels of litter masses [95]. Simultaneously, the variety of fungal communities in leaf litter decomposition is also high [102,116,119–121]. This matter was previously discussed by [83] to build up evidence towards host-recurrence and -specificity of decomposer taxa. Yet less evidence on host-specificity could be recorded within such ecosystems, given that colonization and frequencies of saprobic fungi might be limited [122]. In contrast, [102] and [123] stated leaf litter saprobes can be recurrent and specific towards selected hosts and stages of decomposition. This observation was further supported by the study conducted by [67] on different decomposition stages of leaf litter of *Manglietia garrettii*. It was also described that the host-recurrence of saprobes can be strongly influenced by leaf characteristics rather than host phylogeny, unlike host-pathogen relationships [102]. Evidence from [89] highlighted that microfungal overlap is higher in distantly related host species than in closely related ones. Contradicting this statement, [30] reported that even the phylogenetically closely associated hosts harbour different compositions of saprobic fungi. Yet, the closely related host genera accommodate a higher similarity of dominant fungal taxa than the concerned host families (Figure 1).

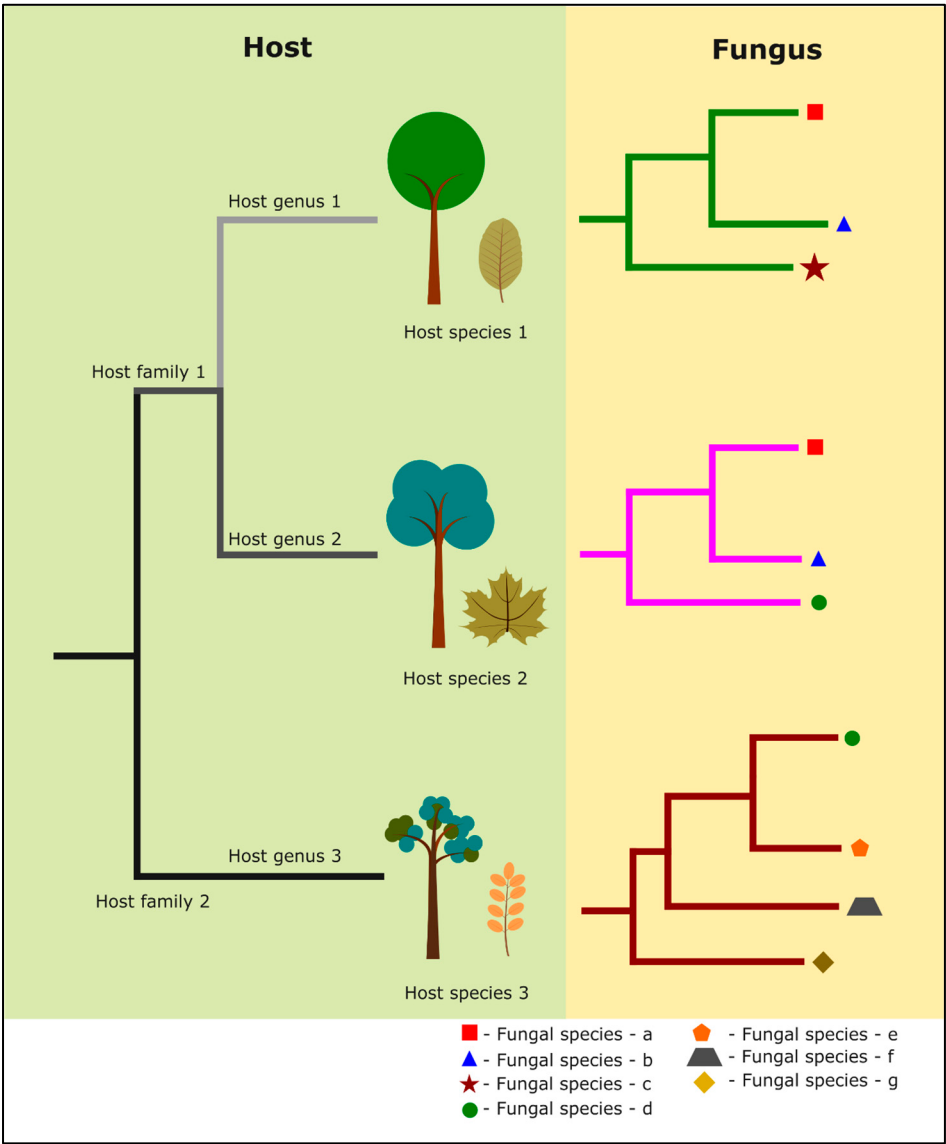


Figure 1. The illustration provides a detailed depiction of the host-preference of leaf litter inhabiting fungi on different host species with relation to host phylogeny. It highlights that taxonomically related hosts harbour more similar fungal communities than those that are far-related. On the left side of the diagram, three distinct host plants belong to three different host genera and two different host families are represented. The right side features the fungal species, each uniquely symbolized by a distinct shape and colour. The first host tree at the top is inhabited by fungal species a, b, and c. The second host tree in the middle harbours fungal species a, b, and d. The third host tree at the bottom is inhabited by fungal species d, e, f, and g.

Understanding the host-preference of saprobic microfungi needs elucidation through different levels of taxonomic hierarchy occupying single to multiple hosts [91,124,125]. Host-preference and recurrence of fungi towards a host family, genus, tissue, geographical distributions, and tree phylogeny have exemplified evidence towards this matter [30,91,123,124]. These studies provide evidence towards saprobic fungi and their preferential occurrence on hosts, substrata or tissues indicating possible host-preference, -recurrence or -specificity. Further studies occupying multiple host species with phylogenetic relatedness simultaneously considering their occurrence in different localities can be utilized to reveal the undescribed and poorly described saprobic fungal taxa to a greater extent.

5. Global Scenario of Leaf Litter-Inhabiting Microfungi

According to estimates by [126] and [127], 2 to 11 million fungi occur worldwide [25]. The documentation of fungi in each region contributes towards predicting the global fungal numbers [25]. Leaf-litter is a dynamic substratum harbouring a range of saprobes throughout the decomposition process, resulting in higher levels of fungal diversity and simultaneously increasing the fungal numbers [59,87,98,116,128]. The majority of studies focused on single hosts and a few hosts, mainly in tropical regions, including Australia, Brazil, Hong Kong, India, Thailand, and China with host species ranging from *Manglietia garrettii*, *Neolitsea dealbata*, *Ficus pleurocarpa*, *Castanopsis diversifolia*, *Magnolia liliifera*, *Shorea obtusa*, *Hevea brasiliensis*, *Anacardium occidentale*, *Clusia nemorosa*, *Vismia guianensis*, *Pavetta indica*, *Celtis formosana*, *Ficus ampelas*, *F. septica*, *Macaranga tanarius*, and *Morus australis* [67,87,98,129–137]. Sub-tropical to temperate region studies on leaf litter-inhabiting microfungi were mainly documented in Japan by [138], focusing on *Camellia japonica* and on *Fagus sylvatica*[103], *Quercus petrea*, *Picea abies*, *Pseudotsuga menziesii* [139] from France, on *Quercus petraea* [39] in Czech Republic and on *Fagus sylvatica* [94] in Germany. Further adding, fungal diversity was documented in New Zealand on *Agathis australis* leaf-litter by [107], on grasses and sedges of *Poaceae* and *Cyperaceae* hosts in Hong Kong by [111] and [140]. Studies representing the southern hemisphere were mainly carried out in South Africa on two plant families *Proteaceae* and *Restionaceae* as exemplified by [141] and [142], respectively. As the previous evidence suggests, most of the leaf litter inhabiting fungal studies have been carried out in tropical regions rather than temperate regions and might be due to the abundance of tropical forests with high litter fall and favourable climate conditions for fungal prevalence. In Table 1 we compare 260 fungal taxa reported on ten hosts in tropical regions [30,87,97,98,119] and present the overlap. The fungal taxa were reported in fungal species and fungal genus levels in these studies therefore the overlap was calculated in fungal species and fungal generic levels. The results indicate that each host species harbours a unique fungal community. Out of the 260 fungal taxa, 18 fungal taxa are unique to *Neolitsea dealbata* (*Lauraceae*), 33 *Ficus pleurocarpa* (*Moraceae*), 22 *Ficus ampelas* (*Moraceae*), 27 *Celtis formosana* (*Lauraceae*), 21 *Macaranga tanarius* (*Euphorbiaceae*), and *Cryptocarya mackinnoniana* (*Lauraceae*), 3 *Darlingia ferruginea* (*Proteaceae*), 7 *Elaeocarpus angustifolius* (*Elaeocarpaceae*), 1 *Ficus destruens* (*Moraceae*), and 12 *Opisthiolepis heterophylla* (*Proteaceae*). The number of overlapping taxa among ten hosts varied from 1 to 20 with the highest overlap recorded between *F. pleurocarpa* (*Moraceae*) and *C. mackinnoniana* (*Lauraceae*) followed by *Ficus pleurocarpa* (*Moraceae*) and *O. heterophylla* (*Proteaceae*) with an overlap of 18 fungal taxa, whereas lower overlap was recorded between the other hosts, respectively. Most overlapping fungal taxa among the 10 hosts are *Acremonium* sp., *Aspergillus* sp., *Beltrania rhombica*, *Beltraniella portoricensis*, *Chaetospermum* sp., *Cladosporium* sp., *Dictyochaeta simplex*, *Dictyochaeta* sp., *Helicosporium* sp., *Idriella cognizarii*, *Parasymphodiella elongata*, *Penicillium* sp., *Pestalotiopsis* sp., *Phoma* sp., and *Selenosporella* species. However, only four of these were identified to species level indicating that they might not be overlapping species. Subsequent evidence suggests the presence of fungal recurrence/preference or specificity among the studied hosts where the fungal overlap is lower compared to the number of unique fungal taxa recorded from each host species thus indicating that litter fungi are far more diverse than realized. A recent study provides similar results with lower fungal overlap on leaf litter across five different hosts [30] further corroborating the topic under concern.

Table 1. Fungal taxa reported on ten different host species and their overlap. Grey highlights the overlapped taxa.

Taxon name	ND (<i>Lauraceae</i>)	FP (<i>Moraceae</i>)	FA (<i>Moraceae</i>)	CF (<i>Lauraceae</i>)	MT (<i>Euphorbiaceae</i>)	CM (<i>Lauraceae</i>)	DF (<i>Proteaceae</i>)	EA (<i>Elaeocarpaceae</i>)	FD (<i>Moraceae</i>)	OH (<i>Proteaceae</i>)
<i>Acremonium</i> sp.	✓	✓				✓	✓	✓	✓	
<i>Acrocalymma ampeli</i>			✓							
<i>Alternaria burnsii</i>					✓					

<i>Alternaria pseudoeichhorniae</i>					✓						
<i>Anthostomella clypeata</i>	✓										
<i>Anthostomella reniformis</i>		✓									
<i>Appendiculella</i> sp.				✓							
<i>Arthrinium hydei</i>				✓							
<i>Arthrinium sacchari</i>					✓						
<i>Arthrinium</i> sp.	✓										
<i>Arxiella celtidis</i>				✓							
<i>Aspergillus</i> sp.	✓		✓	✓	✓						
<i>Asteridiella</i> sp.					✓						
<i>Asterina</i> sp.		✓					✓				
<i>Auxarthron</i> sp.							✓				
<i>Backusella</i> sp.			✓								
<i>Bartalinia robillardoides</i>				✓							

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Beltrania concurvispora</i>		✓							✓	✓
<i>Beltrania rhombica</i>	✓	✓	✓			✓		✓	✓	
<i>Beltrania</i> sp.	✓									
<i>Beltraniella portoricensis</i>	✓	✓				✓	✓	✓	✓	
<i>Beltraniella</i> sp.	✓					✓				
<i>Botryodiplodia theobromae</i>							✓			
<i>Brooksia tropicalis</i>		✓					✓			✓
<i>Camposporium</i> sp.	✓									
<i>Catenosubulispora</i> sp.						✓				
<i>Cephalosporiopsis</i> sp.		✓				✓		✓		
<i>Ceramothyrium longivolcaniforme</i>			✓							
<i>Cercophora fici</i>			✓							
<i>Chaetopsina fulva</i>		✓				✓				
<i>Chaetospermum camelliae</i>		✓								
<i>Chaetospermum</i> sp.						✓	✓	✓	✓	✓
<i>Chaetosphaeria</i> sp.		✓								

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
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Taxon name	ND (<i>Lauraceae</i>)	FP (<i>Moraceae</i>)	FA (<i>Moraceae</i>)	CF (<i>Lauraceae</i>)	MT (<i>Euphorbiaceae</i>)	CM (<i>Lauraceae</i>)	DF (<i>Proteaceae</i>)	EA (<i>Elaeocarpaceae</i>)	FD (<i>Moraceae</i>)	OH (<i>Proteaceae</i>)
<i>Chalara</i> sp.	✓					✓		✓		
<i>Circinotrichum falcatisporum</i>										✓
<i>Circinotrichum maculiforme</i>		✓								
<i>Circinotrichum</i> sp.										✓
<i>Cladosporium cladosporioides</i>	✓									
<i>Cladosporium</i> sp.		✓		✓	✓	✓		✓		✓
<i>Cladosporium tenuissimum</i>					✓					
<i>Coccomyces cf.limitatus</i>								✓		
<i>Coelomycete</i> sp.	✓	✓		✓						
<i>Colletotrichum celtidis</i>				✓						
<i>Colletotrichum fici</i>			✓							
<i>Colletotrichum</i> sp.	✓	✓							✓	
<i>Coniella quercicola</i>			✓	✓						
<i>Conioscypha</i> sp.						✓				

Cryptophiale <i>cf.guadalcanensis</i>							✓			
Cryptophiale <i>kakombensis</i>						✓	✓		✓	
<i>Curvularia</i> sp.		✓							✓	

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Gnomonia elaeocarpa</i>								✓		
<i>Gnomonia queenslandica</i>								✓		
<i>Dischloridium</i> sp.						✓		✓	✓	
<i>Discosia celtidis</i>				✓						
<i>Discosia querci</i>			✓							
<i>Meliola</i> sp.		✓			✓					
<i>Memnoniella alishanensis</i>					✓					
<i>Myrothecium lachatrae</i>		✓								
<i>Parasympodiel la laxa</i>									✓	✓
<i>Paraceratocladium</i> sp.						✓				
<i>Parasympodiel la elongate</i>						✓	✓	✓	✓	✓
<i>Phoma</i> sp.	✓	✓	✓	✓	✓			✓		✓
<i>Phomopsis</i> sp.		✓								✓

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Dematiocladium celtidicola</i>				✓						
<i>Dendrosporium lobatum</i>		✓							✓	
<i>Diaporthe celtidis</i>				✓						
<i>Diaporthe limonicola</i>			✓							
<i>Diaporthe millettiae</i>				✓						
<i>Diaporthe pseudophoenicicola</i>			✓							
<i>Diaporthosporella macarangae</i>					✓					
<i>Dictyoarthrinium africanum</i>	✓									
<i>Dictyochaeta cf.novae-guineensis</i>						✓		✓		
<i>Dictyochaeta</i> sp.	✓	✓				✓		✓		
<i>Dictyocheiropora garethjonesii</i>					✓					

<i>Gliocladiopsis</i> sp.						✓	✓		✓	✓
<i>Gliocladiopsis</i> <i>tenuis</i>		✓						✓		
<i>Gliocladium</i> <i>solani</i>		✓								
<i>Gliocladium</i> sp.	✓	✓								✓
<i>Gliomastix</i> <i>elasticae</i>		✓								
<i>Gliomastix</i> <i>murorum</i>		✓								✓
<i>Gliomastix</i> <i>luzulae</i>										✓
<i>Gliomastix</i> <i>macrocerealis</i>		✓								
<i>Gliomastix</i> sp.										✓

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Ijuhya aquifolii</i>										✓
<i>Ijuhya</i> <i>leucocarpa</i>										✓
<i>Iodosphaeria</i> <i>phyllophila</i>	✓									
<i>Iodosphaeria</i> sp.						✓		✓		
<i>Isthmolongispor</i> <i>a intermedia</i>						✓				
<i>Kramasamuha</i> <i>cf. sibika</i>							✓	✓		
<i>Kylindria</i> sp.						✓				
<i>Lachnum</i> sp.						✓	✓			
<i>Lanceispora</i> <i>amphibia</i>		✓							✓	
<i>Lasiodiplodia</i> <i>thailandica</i>			✓							
<i>Lasiodiplodia</i> <i>theobromae</i>				✓						
<i>Lauriomyces</i> <i>helicocephala</i>								✓		
<i>Leptospora</i> <i>macarangae</i>					✓					
<i>Leptothyrium</i> sp.		✓								
<i>Longihyalospora</i> <i>ampeli</i>			✓							
<i>Marasmius</i> sp.						✓	✓			✓

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Myrothecium</i> sp.	✓									
<i>Neoanthostomella</i> <i>a fici</i>			✓							
<i>Neodictyosporium</i> <i>m macarangae</i>					✓					

Neofusicoccum moracearum	✓									
Neopestalotiopsis asiatica				✓						
Niesslia sp.	✓									
Nigrospora macarangae					✓					
Nigrospora panici	✓									
Nodulisporium sp.	✓									
Oblongihyalospora macarange					✓					
Ochroconis humicola	✓									
Oidiodendron tenuissimum										✓
Ophioceras chiangdaoense				✓						
Ophiognomonina elasticae	✓								✓	
Ophiognomonina sp.						✓	✓		✓	✓
Strigula multiformis				✓						

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
Memnoniella celtidis				✓						
Memnoniella echinata					✓					
Menisporopsis theobromae	✓					✓				
Microdochium phragmites		✓								
Microdochium sp.		✓				✓				
Micropeltis fici			✓							
Micropeltis ficinae			✓							
Minimidochium microsporum						✓				
Mollisia sp.						✓				
Mortierella sp.			✓							
Mucor racemosus				✓						
Mucor sp.	✓			✓						
Muyocopron celtidis				✓						
Muyocopron dipterocarpi				✓						
Muyocopron lithocarpi				✓						
Mycena sp.				✓			✓			

<i>Mycosphaerella</i> sp.			✓							
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Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Parasymphodiella</i> sp.		✓								
<i>Parawiesneriomyces</i> <i>cheschii</i>					✓					
<i>Penicillium</i> sp.	✓	✓	✓		✓			✓		✓
<i>Periconia</i> <i>alishanica</i>					✓					
<i>Periconia</i> <i>byssoides</i>					✓					
<i>Periconia celtidis</i>					✓					
<i>Periconia</i> sp.	✓		✓							
<i>Pestalotiopsis</i> <i>versicolor</i>	✓									
<i>Pestalotiopsis</i> <i>brevisetata</i>		✓								
<i>Pestalotiopsis</i> <i>dracaenea</i>				✓						
<i>Pestalotiopsis</i> <i>papuana</i>				✓						
<i>Pestalotiopsis</i> sp.	✓						✓	✓	✓	✓
<i>Pestalotiopsis</i> <i>trachycarpicola</i>				✓						
<i>Phaeoisaria</i> sp.		✓								
<i>Phaeosphaeria</i> <i>ampeli</i>			✓							
<i>Phialocephala</i> <i>bactrospora</i>								✓		

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
<i>Phyllosticta</i> <i>capitalensis</i>				✓						
<i>Phyllosticta</i> sp.	✓		✓		✓					
<i>Polyscytalum</i> sp.		✓								
<i>Pseudobeltrania</i> sp.							✓			
<i>Pseudomicrodochium</i> <i>antillarum</i>						✓			✓	
<i>Pseudoneottiospora</i> <i>cannabina</i>				✓						
<i>Pseudopestalotiopsis</i> <i>camelliae-sinensis</i>			✓							
<i>Pseudopithomyces</i> <i>chartarum</i>					✓					
<i>Pseudorobillarda</i> <i>phragmitis</i>				✓						
<i>Pseudospiropes</i> <i>pinarensis</i>		✓								
<i>Pyricularia</i> sp.						✓				

Thozetella sp.	✓						✓			
Thysanophora sp.	✓									
Torula fici				✓						
Torula sp.	✓									
Trichoderma sp.	✓	✓			✓					
Trichoderma viride		✓						✓		✓
Trichothecium sp.		✓								
Verticillium sp.		✓				✓				✓
Verticimonosporium ellipticum						✓				
Volutella ramkurii		✓								

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
Wiesneriomyces javanicus	✓	✓				✓				
Wiesneriomyces laurinus			✓							
Wiesneriomyces sp.	✓	✓								
Yunnanomyces pandanicola			✓							
Zygosporium echinosporium		✓				✓				✓
Zygosporium mansonii		✓								✓
Zygosporium sp.			✓	✓	✓					
Xylaria sp.		✓								
Dactylaria ficusicola		✓							✓	
Dictyochaeta simplex						✓	✓	✓	✓	✓
Dactylaria belliana		✓								✓
Dactylaria section Mirandina sp.						✓				
Dactylaria sp.	✓	✓						✓		
Dactylella sp.		✓								
Cylindrocarpon cf.ianthothele										✓
Stachybotrys sp.	✓							✓		
Stilbella sp.						✓	✓			

Taxon name	ND (Lauraceae)	FP (Moraceae)	FA (Moraceae)	CF (Lauraceae)	MT (Euphorbiaceae)	CM (Lauraceae)	DF (Proteaceae)	EA (Elaeocarpaceae)	FD (Moraceae)	OH (Proteaceae)
Wiesneriomyces javanicus	✓	✓				✓				
Wiesneriomyces laurinus			✓							
Wiesneriomyces sp.	✓	✓								

<i>Yunnanomyces pandanicola</i>		✓							
<i>Zygosporium echinosporium</i>	✓				✓				✓
<i>Zygosporium mansonii</i>	✓								✓
<i>Zygosporium</i> sp.		✓	✓	✓					
<i>Xylaria</i> sp.	✓								
<i>Dactylaria ficusicola</i>	✓							✓	
<i>Dictyochaeta simplex</i>					✓	✓	✓	✓	✓
<i>Dactylaria belliana</i>	✓								✓
<i>Dactylaria</i> section <i>Mirandina</i> sp.					✓				
<i>Dactylaria</i> sp.	✓	✓					✓		
<i>Dactylella</i> sp.	✓								
<i>Cylindrocarpon cf.ianthothele</i>									✓
<i>Volutella</i> sp.		✓			✓				
<i>Wardomyces</i> sp.	✓								

ND = Neolitsea dealbata, FP = Ficus pleurocarpa, FA = Ficus ampelas, CF = Celtis formasana, MT = Macaranga tanarius, CM = Cryptocarya mackinnoniana, DF = Darlingia ferruginea, EA = Elaeocarpus angustifolius, FD = Ficus destruens, OH = Opisthiolepis heterophylla. Dataset was adopted from the previous studies conducted by [87] and [30].

In Table 2 we compare the fungi in 10 different families which include *Anacardiaceae*, *Dipterocarpaceae*, *Eleocarpaceae*, *Euphorbiaceae*, *Fagaceae*, *Lauraceae*, *Magnoliaceae*, *Moraceae*, *Proteaceae*, and *Rubiaceae* [87,97,98,131,133,135–137]. Accordingly, the fungal consortium specifically on leaf litter found to be quite similar which means that litter as a substrate facilitates a common group of fungi that can be present in variable degrees across different hosts and related families. Focused families in Table 2 show different numbers of fungal taxa, ranging from 91 taxa on *Fagaceae* and 54 taxa on *Rubiaceae* as the highest and the lowest number of taxa reported on *Dipterocarpaceae* and *Proteaceae* (25 and 27 taxa, respectively). Different numbers suggest that the capacity of each host family can vary in harboring litter saprobes. The tree species, leaf litter chemistry, and seasonal variations can be influential towards the number, composition and diversity of litter saprobes dwelling upon each host [30,132].

Estimating the current number of fungi has always been topical; thus, the latest working estimate is 2.2–3.8 million species [126], whereas [143] discussed the potential of elucidating higher numbers of undescribed species compared to the 6.8% to 3.9% of currently known or described species [143–145]. Estimating the fungal numbers can be supported by further studies related to fungal hosts or tissue specificity at various levels in host phylogeny, along with adapting appropriate methodologies in taxonomic elucidations unaltering the diversity estimates [91].

Evaluating the previous studies on leaf litter fungi as discussed above, it is evident that number of unique fungi within each host/family are much higher than the initially proposed ratio of 6:1 (fungal taxa per one plant) by [146] and the recently extrapolated 9.8:1 (fungal taxa per one plant) [126]. As per the comparisons made herein across 10 different hosts, a ratio of 47:1 (470 fungi and 10 plants) is suggested for redefining the host fungal ratios. This value is extrapolated by reviewing the previous work elucidating saprobic fungi specifically on leaf litter mainly in the tropics. Further, the ratio extrapolated herein is specified to saprobes dwelling on leaf litter therefore an overall estimate for host-to-fungal ratio can go much higher considering a summation of pathogens, endophytes, leaf and woody litter saprobes dwelling on a specific host. Relying on the proposed ratio herein, future estimates for global fungal numbers can be extrapolated much more accurately.

Table 2. Comparison of the fungi reported on 10 different host families.

Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
1	Anacardiaceae	<i>Anacardium occidentale</i>	India	48	[135,137]
		<i>Dactylaria biseptata</i> , <i>Dicyma vesiculifera</i> , <i>Emericella nidulans</i> , <i>Fusarium dimerum</i> , <i>Fusarium oxysporum</i> , <i>Gibberella bacata</i> , <i>Gloeosporium musarum</i> , <i>Glomerella tucumanensis</i> , <i>Gyrophthrix circinata</i> , <i>Gyrophthrix podosperma</i> , <i>Hansfordia pulvinata</i> , <i>Henicospora coronata</i> , <i>Idriella lunata</i> , <i>Khuskia oryzae</i> , <i>Lasiodiplodia theobromae</i> , <i>Leptosphaerulina chartarum</i> , <i>Meliola</i> sp., <i>Memnoniella echinata</i> , <i>Metulocladosporiella musae</i> , <i>Paecilomyces carneus</i> , <i>Parasymphodiella laxa</i> , <i>Penicillium citrinum</i> , <i>Penicillium funiculosum</i> , <i>Penicillium oxalicum</i> , <i>Penicillium verruculosum</i> , <i>Pestalotiopsis theae</i> , <i>Phaeotrichoconis crotalariae</i> , <i>Pithomyces maydis</i> , <i>Polyscytalum fecundissimum</i> , <i>Pseudobeltrania penzigii</i> , <i>Pseudocochliobolus eragrostidis</i> , <i>Scolecobasidium tshawytschae</i> , <i>Selenodriella fertilis</i> , <i>Selenospora curvispora</i> , <i>Setosphaeria rostrata</i> , <i>Stachybotrys chartarum</i> , <i>Staphylotrichum coccosporum</i> , <i>Subramaniomyces fusisaprophyticus</i> , <i>Thozetella tocklaiensis</i> , <i>Torula herbarum</i> , <i>Trichoderma harzianum</i> , <i>Trichoderma viride</i> , <i>Trichothecium roseum</i> , <i>Volutella ciliata</i> , <i>Wiesneriomyces laurinus</i> , <i>Zygosporeum gibbum</i> , <i>Zygosporeum masonii</i> , <i>Zygosporeum oscheoides</i>			
Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
2	Magnoliaceae	<i>Magnolia liliifera</i>	Thailand	47	[97]
		<i>Albonectria rigidiuscula</i> , <i>Anthostomella monthadoia</i> , <i>Anthostomella tenacis</i> , <i>Bionectria ochroleuca</i> , <i>Bionectria palmicola</i> , <i>Bionectria</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>Colletotrichum</i> sp., <i>Corynespora cassiicola</i> , <i>Cylindrocladium floridanum</i> , <i>Dactylaria dimorphospora</i> , <i>Dactylaria longidentata</i> , <i>Dokmaia monthadangii</i> , <i>Fusarium</i> sp., <i>Giugnardia</i> sp., <i>Gliocladium</i> sp., <i>Guignardia mangiferae</i> , <i>Haematonectria haematococca</i> , <i>Hyponectria manglietiae</i> , <i>Hyponectria manglietiagarrettii</i> , <i>Hyponectria</i> sp., <i>Hyponectria suthepensis</i> ,			

Hypoxyton sp., *Ijuhya parilis*, *Leptosphaeria* sp., *Munkovalsaria appendiculata*,
Hyponectria manglietiagarrettii, *Hyponectria* sp., *Hyponectria suthepensis*,
Hypoxyton sp., *Ijuhya parilis*, *Leptosphaeria* sp., *Munkovalsaria appendiculata*,
Munkovalsaria magnoliae, *Nectria haematococca*, *Nectria* sp., *Periconia*
jabalpurensis, *Phaeosphaeria* sp., *Phoma* sp., *Phomopsis* sp., *Phyllosticta*
capitaliensis, *Physalospora* sp., *Pseudohalonectria suthepensis*, *Rhytisma* sp.,
Sporidesmium crassissporum, *Stachybotrys parvispora*, *Volutella* sp.

Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
3	Fagaceae	<i>Acremonium</i> sp., <i>Albonectria albosuccinea</i>, <i>Alternaria</i> sp., <i>Annulatascaceae</i> sp., <i>Ardhachandra cristaspora</i>, <i>Arthrinium</i> sp., <i>Aspergillus</i> sp., <i>Asterina</i> sp., <i>Bacillispora aquatica</i>, <i>Beltrania mangiferae</i>, <i>Beltrania rhombica</i>, <i>Beltraniella</i> <i>odinae</i>, <i>Beltraniella portoricensis</i>, <i>Beltraniella</i> sp., <i>Bipolaris cynodontis</i>, <i>Cercosporula</i> sp., <i>Chaetendophragmia triangularia</i>, <i>Chaetosphaeria</i> sp., <i>Chalara</i> <i>pteridina</i>, <i>Cladosporium cladosporioides</i>, <i>Cladosporium oxysporum</i>, <i>Cladosporium</i> sp., <i>Cladosporium sphaerospermum</i>, <i>Cladosporium tenuissimum</i>, <i>Clonostachys candelabrum</i>, <i>Clonostachys compactiuscula</i>, <i>Coelomycete</i> sp., <i>Cryptophiale udagavae</i>, <i>Cylindrocladium gracile</i>, <i>Cylindrocladium</i> <i>pseudogratile</i>, <i>Cylindrum griseum</i>, <i>Dendrodochium cylindricum</i>, <i>Dictyochaeta</i> <i>cylindrospora</i>, <i>Dictyochaeta heteroderae</i>, <i>Dictyochaeta simplex</i>, <i>Dictyochaeta</i> <i>sp.</i>, <i>Dictyochaeta stipiticolla</i>, <i>Emarcea castanopsidicola</i>, <i>Endophragmiella</i> sp., <i>Fusarium</i> sp., <i>Geotrichum candidum</i>, <i>Gnomonia gnomon</i>, <i>Hansfordia</i> sp., <i>Haplographium</i> sp., <i>Helicosporium talbotii</i>, <i>Hyponectria buxi</i>, <i>Idriella fertilis</i>, <i>Idriella</i> sp., <i>Kionochaeta spissa</i>, <i>Kramasamuha sibika</i>, <i>Lachnum</i> sp., <i>Lauriomyces bellulus</i>, <i>Lecanicillium lecanii</i>, <i>Lichenopeltella salicis</i>, <i>Lophodermium australiense</i>, <i>Lophodermium</i> sp., <i>Marasmius</i> sp., <i>Menisporopsis</i> <i>novaezelandiae</i>, <i>Microdochium phragmitis</i>, <i>Microthyrium</i> sp., <i>Monochaetia</i> sp., <i>Mycena</i> sp., <i>Mycosphaerella</i> sp., <i>Oedocephalum</i> sp., <i>Ophioceras commune</i>, <i>Parasymphodiella laxa</i>, <i>Penicillium</i> sp., <i>Periconia cookei</i>, <i>Periconia paludosa</i>, <i>Periconia</i> sp., <i>Pestalotia hansenii</i>, <i>Pestalotiopsis tecomicola</i>, <i>Phaeoisaria</i> <i>sp.</i>, <i>Phomopsis</i> sp., <i>Pithomyces karoo</i>, <i>Pseudobotrytis terrestris</i>, <i>Pseudohalonectria phialidica</i>, <i>Ramularia gei</i>, <i>Stemonitis</i> sp., <i>Stictis</i> sp., <i>Stomiopeltis</i> sp., <i>Subramaniomyces fusisaprophyticus</i>, <i>Subulispora procuroata</i>	Thailand	91	[131]

Thozetella sp., *Thysanophora* sp., *Tritirachium bulbophorum*, *Verticillium* sp.,
Wiesneriomyces javanieus, *Xenocylindrocladium* sp., *Zygosporium gibbum*,
Zygosporium minus

Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
4	Rubiaceae	<i>Pavetta indica</i>	India	54	[136]
5	Dipterocarpaceae	<i>Shorea obtusa</i>	Thailand	25	[133]

sp., *Talaromyces* sp., *Trichoderma asperellum*, *Trichoderma hamatum*, *Xylaria* sp.

Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
6	Lauraceae	<i>Neolitsea dealbata</i>	Australia	48	[87]
7	Moraceae	<i>Ficus ampelas</i>	China	34	[30]
8	Euphorbiaceae	<i>Macaranga tanarius</i>	China	30	[30]

Dictyocheiropora garethjonesii, *Hermatomyces biconisporus*,
Hermatomyces sp., *Idriella* sp., *Leptospora macarangae*,

Family	Species	Recorded fungal taxa	Country	Number of fungal taxa	References
		<i>Meliola</i> sp., <i>Memmoniella alishanensis</i> , <i>Memmoniella echinata</i> , <i>Neodictyosporium macarangae</i> , <i>Nigrospora macarangae</i> , <i>Oblongihyalospora macarangae</i> , <i>Parawiesneriomyces chiayiense</i> , <i>Penicillium</i> sp., <i>Periconia alishanica</i> , <i>Periconia byssoides</i> , <i>Periconia celtidis</i> , <i>Phoma</i> sp., <i>Phyllosticta</i> sp., <i>Pseudopithomyces chartarum</i> , <i>Stachybotrys aloeticola</i> , <i>Zygospodium</i> sp.			
9	<i>Proteaceae</i>	<i>Darlingia ferruginea</i>	Australia	27	[87]
		<i>Acremonium</i> sp., <i>Beltraniella portoricensis</i> , <i>Botryodiplodia theobromae</i> , <i>Brooksia tropicalis</i> , <i>Chaetospermum</i> sp., <i>Cryptophiale cf. guadalcanensis</i> , <i>Cryptophiale kakombensis</i> , <i>Cylindrocladium coulhouiivar.coulhounii</i> , <i>Dictyochaeta simplex</i> , <i>Gliocladiopsis</i> sp., <i>Harpographium</i> sp., <i>Helicosporium</i> sp., <i>Hyponectria</i> sp., <i>Ijuhya aquifolii</i> , <i>Kramasamuha cf. sibika</i> , <i>Lachnum</i> sp., <i>Marasmius</i> sp., <i>Mycena</i> sp., <i>Ophiognomonina</i> sp., <i>Parasymphodiella elongata</i> , <i>Pestalotiopsis</i> sp., <i>Pseudobeltrania</i> sp., <i>Selenosporella cristata</i> , <i>Selenosporella</i> sp., <i>Stilbella</i> sp., <i>Thozetella gigantea</i> , <i>Thozetella</i> sp.			
10	<i>Elaeocarpaceae</i>	<i>Elaeocarpus angustifolius</i>	Australia	39	[87]
		<i>Acremonium</i> sp., <i>Beltrania rhombica</i> , <i>Beltraniella portoricensis</i> , <i>Cephalosporiopsis</i> sp., <i>Chaetospermum</i> sp., <i>Chalara</i> sp., <i>Cladosporium</i> sp., <i>Coccomyces cf. limitatus</i> , <i>Cylindrocladium coulhouiivar.coulhounii</i> , <i>Cylindrocladium floridanum</i> , <i>Dactylaria</i> sp., <i>Dictyochaeta cf. novae-guineensis</i> , <i>Dictyochaeta simplex</i> , <i>Dictyochaeta</i> sp., <i>Dischloridium</i> sp., <i>Gliocephalotrichum simplex</i> , <i>Gliocladiopsis tenuis</i> , <i>Gnomonia elaeocarpa</i> , <i>Gnomonia queenslandica</i> , <i>Guignardia</i> sp., <i>Hansfordia pulvinata</i> , <i>Harpographium</i> sp., <i>Idriella acerosa</i> , <i>Idriella cagnizarii</i> , <i>Iodosphaeria</i> sp., <i>Kramasamuha cf. sibika</i> , <i>Lauriomyces helicocephala</i> , <i>Parasymphodiella elongata</i> , <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phialocephala bactrospora</i> , <i>Phoma</i> sp., <i>Scolecobasidium cf. fusiforme</i> , <i>Scolecobasidium</i> sp., <i>Selenodriella</i> sp., <i>Selenosporella cristata</i> , <i>Selenosporella</i> sp., <i>Stachybotrys</i> sp., <i>Trichoderma viride</i>			

6. Methods of Studying Leaf Litter Inhabiting Microfungi

Currently, litter fungal research primarily uses culture-dependent and culture-independent approaches [33,39,67,87,97,116,131,132,137,147–150]. Culture-dependent methods follow the traditional flow of observing fruiting structures [Conidiomata (pycnidial or acervuli) ascomata, hyphomycetes] on leaf litter with successive steps of sectioning or picking and mounting on slides for photomicrographs followed by single germinated spore isolation in obtaining axenic cultures through a spore suspension on PDA within 24 hours [149]. Most recent taxonomic elucidations associated with litter fungi followed the single spore isolation method [98,151,152].

Culture-dependent methods result in pure cultures of fungal taxa, which will be a source of DNA, in turn supporting PCR amplification of fungal-specific primers and molecular phylogenetics [153,154]. Moreover, a physical sample can be linked to ecology and host substrates, a source for storage and reproducibility, as a preservation method as a dried culture is found to be advantageous in a taxonomic sense [155–164]. Despite the stated advantages, fungal isolations are challenging given the fact that many litter fungi are non-culturable or dormant, thereby underestimating the real fungal numbers colonizing the substrates [33,116,158,165]. Culture-independent methods involve direct extraction of DNA from leaf-litter substrates identified as eDNA or environmental DNA in revealing unculturable fungal taxa [154], and the generated data pass through vigorous analysis pipelines, including metagenetic, metagenomics (DNA-based), and meta-transcriptomics (RNA-based) approaches [166,167]. Presently, high-throughput sequencing (HTS) is the current most up-to-date third-generation sequencing (TGS) technique that utilizes eDNA-based fungal data in profiling taxonomic communities on environmental samples [168–173]. This method was found to be quite advantageous in revealing unculturable and hidden fungal taxa, unveiling sexual-asexual relationships, delimiting taxa in higher taxonomic levels, evolutionary relationships, and chemotaxonomy [163,166,170–177].

Relatively fewer studies have highlighted elaborating the leaf litter inhabiting fungi through HTS and metabarcoding. 1,874 operational taxonomic units (OTUs) belonging to 387 fungal genera from oak leaves were revealed by [39] unravelling the leaf-litter fungal diversity. A study revealing the fungal composition of alder leaves in Finland classified the fungal OTUs at the genus and species level, resulting in 21 and 32 OTUs, respectively. The composition is dominated by *Basidiomycetes* taxa followed by *Mycosphaerellaceae* taxa, *Aspergillus* sp., *Aureobasidium* sp., *Cryptococcus* sp., *Dioszegia* sp., *Glomeromycota* sp., *Tremellomycetes* sp., and *Wallemia sebi* [178]. Documenting the senescent leaf microbiome and their substrate affinity in the USA on *Carya ovata* and *Acer rubrum* leaf litter resulted in 421 OTUs with a dominance of *Colletotrichum* sp., *Xylariales* sp., *Codinaea lambertiae*, *Ascomycota* sp., *Coleophoma* sp., *Lophiostoma* sp., and *Amorocoelephoma* species [179]. *Acer rubrum* fungal profile included *Lareunionomyces*, *Dothiora*, *Ampelomyces* and *Saitozyma*. Comparably, *Carya ovata* resulted in *Periconia* sp., *Plectosphaerella* sp., and *Mycosphaerella* taxa.

Overlapping taxa for both hosts were *Exobasidium* sp., *Seimatosporium* sp., *Inocybe* sp., *Mortierella* sp., and *Russula* sp., providing evidence for possible fungal host preference [179]. The presence of litter saprobes on *Castanopsis sieboldii* (Fagaceae) documented through metabarcoding revealed dominant OTUs as *Nemania diffusa*, *Nemania bipapillata*, *Gymnopus* sp., *Nodulisporium* sp. belonged to *Xylaria*, *Hypoxylon*, *Nemania*, *Astrocystis*, *Biscogniauxia*, and *Nodulisporium* within *Xylariaceae* (*Sordariomycetes*) apart from the *Basidiomycetes* taxa [180]. In review, some taxa recovered through HTS were rarely documented through culture-based studies of leaf litter fungi by [30,33,87,95,97,104,116] as *Nemania diffusa*, *Nemania bipapillata*, *Plectosphaerella* sp., *Gymnopus* sp., *Wallemia sebi* thus, HTS-based fungal elucidations were able to reveal poorly characterized taxa which are difficult to isolate and maintain as cultures [39,160,173,182].

Limitations of HTS in leaf-litter successional studies are noteworthy to mention, including inadequate species identifications (only up to genus and family), only short regions being amplified with higher variability causing less reliable sequences and in a taxonomic sense causing an increased number of taxa with inconsistent and incomplete data [153,175,181,182]. Given these facts, it can be concluded that occupying culture-independent as well as culture-dependent techniques in equal

proportions will be successful in unravelling the hidden fungal taxa on environmental samples including leaf litter.

7. Conclusions and Future Perspectives

Leaf litter inhabiting saprobes is essential in decomposition and subsequent nutrient recycling [183,184]. Exploring and documenting the complete fungal numbers on litter substrates is challenging [30,185]. Most of the litter fungal studies concentrated on single or multiple hosts together with fungal succession studies yet elucidating the host preference, specificity, or recurrence of saprobes in phylogenetically related hosts is scarce [30,67,87,95,96,116] and subsequent knowledge on levels of diversity generated by studying these factors is still vague. It is imperative that host fungal associations could provide understanding towards predicting global fungal numbers [25,143–145].

Utilizing integrative approaches of culture-dependent and independent methods will be more appropriate in elucidating hidden fungal taxa and diversity in a promising manner [153,154]. Furthermore, extending research on functional associations and chemical profiling, life mode transition, host jumps, and host shifting of microfungi, assessing cryptic species in mostly overlooked or less studied ecological niches would be appropriate research-driven advancements for science and its sustainable utilization in the current omics era [154,186].

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