INVITED REVIEW
doi: 10.2306/scienceasia1513-1874.2025.s014

ScienceAsia 51S (1): 2025: ID 2025s014: **1–13**

The crucial roles of ascomycetes in wood litter decomposition: Current knowledge, diversity and function

Naghmeh Afshari[a,b], **Antonio R. Gomes de Farias**[b], **Maryam T. Noorabadi**[c], **Chitrabhanu S. Bhunjun**[b,d], **Chayanard Phukhamsakda**[b], **Kevin D. Hyde**[b,e,f,∗,†], **Fatimah Alotibi**[f], **Saisamorn Lumyong**[a,g,h,∗,‡]

[a] Department of Biology, Faculty of Sciences, Chiang Mai University, Chiang Mai 50200 Thailand
[b] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100 Thailand
[c] Innovative Institute for Plant Health, College of Agriculture and Biology, Zhongkai University of Agriculture and Engineering, Guangzhou, Guangdong 510225 China
[d] School of Science, Mae Fah Luang University, Chiang Rai 57100 Thailand
[e] Key Laboratory of Phytochemistry and Natural Medicines, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201 China
[f] Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11495 Saudi Arabia
[g] Center of Excellence in Microbial Diversity and Sustainable Utilization, Chiang Mai University, Chiang Mai 50200 Thailand
[h] Academy of Science, The Royal Society of Thailand, Bangkok 10300 Thailand

∗Corresponding authors, e-mail: kdhyde3@gmail.com, scboi009@gmail.com

Received 18 Nov 2024, Accepted 25 May 2025
Available online 25 Jun 2025

ABSTRACT: Plant litter, encompassing fallen branches and leaves, are integral component of forest ecosystems, serving as a critical substrate for microbial colonization and activities. They are primarily decomposed by diverse microorganisms, among them fungi which contribute to the carbon and nutrient cycling in different habitats. Moreover, the diversity of fungi, particularly ascomycetes, is crucial for maintaining ecosystem dynamics and resilience. These fungi can decompose complex organic compounds, which are abundant in wood litter. Wood litter significantly affects biodiversity, carbon storage, and nutrient dynamics, thereby facilitating nutrient recycling and consequently promoting plant growth. Despite the importance of ascomycetes in wood litter decomposition, their diversity and specific ecological functions are difficult to establish. This review highlights the importance of ascomycetes in the decomposition of wood litter, emphasizing their distribution and diversity as fundamental aspects of the ecosystem. Furthermore, this review aims at consolidating existing knowledge on the diversity and ecological roles of ascomycetes in terrestrial wood litter decomposition and identifying gaps in current knowledge. Future research focusing on novel comprehensive molecular approaches coupled with studies on the diversity and host-recurrence of ascomycetes are requisite. Additionally, long-term monitoring of the decomposition process under different environmental conditions is required to properly understand the biological and ecological roles of this group of fungi.

KEYWORDS: fungal diversity, fungal succession, host-recurrence, organic substrates, saprobes, terrestrial woody litter

INTRODUCTION

Fungi substantially contribute to nutrient cycling and overall ecosystem functionality in both terrestrial and aquatic environments. Therefore, their diversity represents a fundamental aspect of ecosystem dynamics [1–3]. They are responsible for breaking down complex organic compounds, such as lignin and cellulose, converting them into simpler forms that other organisms can utilize [4, 5]. Fungi also play an essential role in carbon cycling [6–8]. Fungal populations are significantly influenced by the diversity of plant communities and they conversely impact plant growth through pathogenic and mutualistic behaviors, thus affecting nutrient availability and cycling [9–11].

Plant litter, encompassing fallen branches and leaves, provides an essential substrate facilitating fungal colonization and activity. Fungi possess the capability to generate a broad spectrum of extracellular enzymes, which participate in the degradation of litter [12–14]. Wood litter decomposition, a vital process in forest ecosystems, is significantly influenced by fungal colonization. This process unfolds through a sequential process, characterized by both quantitative and qualitative alterations in fungal communities [5, 15]. Among the diverse organisms involved in this process, fungi, particularly ascomycetes, one of the largest fungal phyla, play a pivotal role. Ascomycetes exhibit remarkable diversity and are able to colonize a broad range of substrates, including wood litter [16, 17].

Despite their importance, our understanding of the diversity of ascomycetes involved in wood litter decomposition and their specific function remains in-

---

[†] World-leading mycologist; Highly Cited Researcher: - in Mycology (Thompson Reuters, 2014–2024), - in Plant and Animal Science (Web of Science, 2016–2024); President of the Asian Mycological Association (2007–2011).

[‡] 2022 NRCT Distinguished Research Professor Awarding Grant; TRF Senior Research Scholar (2010–2016); President of the Asian Mycological Association (2019–2023).

complete. This review aims to consolidate the knowledge regarding the function, diversity, host preference, and role of ascomycetes associated with terrestrial woody litter. We explore recent developments in the field, identify gaps in our current understanding, and suggest potential directions for future research.

IMPORTANCE OF PLANT LITTER

Plant litter (hereafter referred to as litter) is an integral part of forest ecosystems. It refers to fine detrital biomass on the forest floor, including twigs, leaves, fruits, flowers, bark, and buds [18, 19]. In these environments, litter is composed of a complex mixture of dead plant particles originating from different plant species, and it has been defined in various ways [20]. Swift et al [21] defined litter as materials produced through senescence and remaining debris during harvest time. According to Facelli and Pickett [22], litter refers to small-sized dead plant material on the ground, which may or may not be considered part of litter category depending on the research objectives. According to Bremer et al [23], litter is defined as deceased plant material that has become detached from living vegetation; for instance, a dead branch or leaves in a tree crown may begin decomposition before falling to the ground, or tree heartwood may die and decompose before the tree falls. Litter is generally divided into leaf litter and woody debris. Leaf litter, which forms the majority of fallen litter, accounts for 22–81% of the total, with deciduous trees producing 3–5 tons of leaves per hectare in both tropical and temperate forests [2].

On the other hand, woody debris which includes standing dead and coarse fallen trees, and hanging branches and stumps, is often overlooked and plays a significant role in terrestrial and aquatic ecosystems, contributing to detritus biomass in forests, freshwaters, and coastal marine areas, and enhancing forest biodiversity [24, 25]. Woody litter is classified into fine and coarse types. The definitions of these terms vary depending on the context and study. For instance, Tritton [26] defines fine woody debris as pieces smaller than 1 cm and coarse woody debris as pieces larger than 1 cm. Harmon et al [24] describe fine woody debris as woody debris smaller than 10 cm and coarse woody debris as pieces larger than 10 cm in diameter and more than 1 m in length. Wei et al [27] categorize coarse woody debris as being $\geqslant 2.5$ cm and fine woody debris as being smaller than 2.5 cm in diameter. Eaton and Lawrence [28] classify fine woody debris as being $\geqslant 1.8$ cm to $\leqslant 10$ cm in diameter and coarse woody debris as being $\geqslant 10$ cm in diameter.

Woody litter, a key element of the forest floor, enhances habitat diversity, aids tree seedling survival, and serves as a source of energy, carbon, and water. It is a vital nutrient reservoir, with availability dependent on the size and number of debris [29]. It regulates water flow and sediment movement [30], impacts biodiversity [31, 32], and despite low nutrient concentrations, acts as a long-term nutrient pool [33].

The dynamics of coarse woody debris encompass several key aspects, including input characteristics, distribution patterns, their correlation, nutrient dynamics, respiration, decomposition processes, and management strategies [34]. Unmanaged forests tend to have more woody debris compared to managed forests. In the latter, timber harvesting results in a significant amount of woody litter, including branches and twigs, produced by the remaining trees [31]. Indeed, the dynamics of woody debris play a vital role in both carbon cycle and forest ecosystems, yet they are not thoroughly studied. These dynamics contribute to forestry productivity by accumulating organic matter in the soil, retaining moisture, and providing habitats for decomposer organisms and ectomycorrhizal roots. They also enhance biological diversity by offering a seedbed for forest regeneration and supporting a variety of species [24, 34]. From a geomorphological perspective, they increase slope stability, manage storm-induced surface runoff, influence nutrient fluxes, and mitigate the risk of acidification [34, 35]. In clear-cut watersheds, the dynamics of woody debris are essential for conserving nutrients and ensuring system resilience [30].

DECOMPOSITION OF WOODY LITTER

Litter decomposition refers to the breaking down of dead organic matter into progressively smaller particles. This biochemical process is controlled by various chemical, physical, and biological factors [36] (Fig. 1).

This process plays a vital role in the biogeochemical cycling of elements in ecosystems. During this process, the structure of the organic material is gradually broken down until it becomes unrecognizable, and organic molecules are converted into their prime components (water, carbon dioxide, and minerals) (Fig. 2). The initiation of litter decomposition lacks a precise benchmark, and the decomposition rates depend on the types and composition of the litter, potentially leading to the incorporation of diverse chemical and physical components into the soil [22, 37]. Wood litter decomposition is predisposed by a grouping of physical, chemical, and biological factors. Physical factors, for instance, moisture, temperature, and oxygen accessibility, normalize microbial activity and enzymatic functions, with humidity and oxygen accessibility endorsing microbial occupation and aerobic decomposition [19]. Chemical properties like lignin content, nitrogen availability, and pH meaningly affect rottenness rates, as high lignin content (common in coniferous species) slows decomposition, while nitrogen-rich litter hastens microbial interruption [38, 39]. Biological factors, including the composition of fungal and bacterial groups and soil fauna, are serious for decay, with fungi

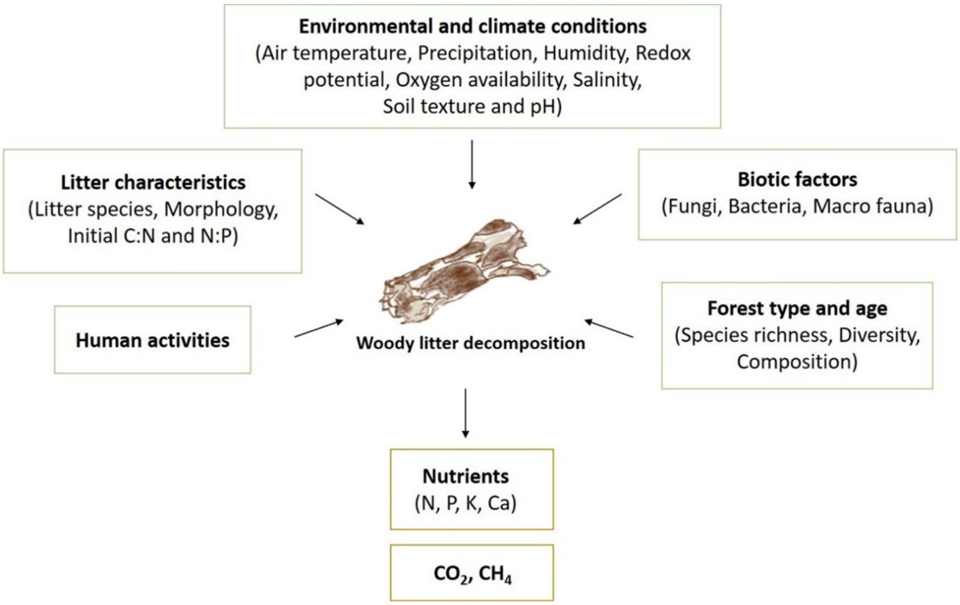

Fig. 1 Simplified diagram showing factors influencing wood litter decomposition and its contribution to carbon and nutrient flows in ecosystem.

like ascomycetes and basidiomycetes breaking down complex organic substances, while soil fauna enhance decomposition by breaking down litter [40]. Furthermore, ecological and climatic factors, such as forest type and climate (temperature, precipitation, etc.), have an impact on microbial dynamic forces and litter quality. Because of differences in microbial variety and litter chemistry, deciduous forests typically exhibit faster decomposition [19]. These factors' interactions with the carbon and nitrogen biogeochemical cycles demonstrate the intricate nature of wood litter decomposition. It is also influenced by the ecological and climatic conditions of the site [41]. The decomposition rates are influenced by climate factors and also depend on the legacy of the plant's functional properties within litter populations. The forest type and neighbouring species significantly impact the rate of decomposition [42]. According to Cornwell et al [43], plant species diversity is more critical in driving decomposition rates than climate differences. They also note a consistent link between a species' litter decomposability and its ecological strategy across diverse global ecosystems.

Litter decomposition drives forest biogeochemical cycles, impacting carbon and nutrient cycling in terrestrial and freshwater environments [2, 44, 45]. It influences vegetation composition and releases carbon dioxide (CO_2) [2, 44] and potassium (K) [46] and enhances the total carbon (C) storage [33]. However, uncertainties exist in biogeochemical models related to carbon fluxes from decaying woody debris [33]. Litter can also significantly affect seed germination and seedling establishment, modulate the physical and chemical properties of soil, and influence interspecific competition on the ground [22, 37, 47, 48]. Belowground litter also plays a significant role as a driver of ecosystem organic matter dynamics [49]. In this regard, litter contributes to the long-term fixation of soil organic matter (SOM) through mineralization and incorporation into the soil mineral layer. Additionally, litter can replace mineral soil horizons in the forest environment, contributing to ecosystem equilibrium and influencing the conditioning of belowground forests [19].

Wood decomposition is generally slow, but it varies depending on the wood type. Small twigs decompose at a similar rate to leaf litter, while logs and trunks can take almost as long as the tree's lifetime to decompose [25]. Logs have a half-life of 6.3 years, while snags have 11.2 years in temperate deciduous forests [50]. All deadwood, including snags or standing dead trees not touching the forest floor, decomposes at rates determined by their position on the tree [25]. In tropical seasonal rainforests in southwest China, logs had the highest decay rate, while large branches and standing dead boles had lower rates [33]. Lignified plant substrate litter, despite its low decomposition rate, significantly contributes to soil organic matter [51].

During the decomposition process, litter undergoes a rapid depletion of soluble compounds such as sugar, amino acids, and starch due to leaching and biological activity in the soil, particularly after certain microbial species degrade lignin and cellulose [2]. The successional process of woody litter decomposition is

Fig. 2 Stages of wood decomposition in terrestrial ecosystem. (a) A recently fallen branch, (b) Initial stage of decay (fragmentation of the bark), (c) Branch's bark has sloughed off, (d) Advanced decomposition, characterized by loss of shape and softening of the inner heartwood.

presented in Fig. 3. Fungi are very important in this process being the main degraders of lignocellulose [52, 53]. The decomposition process of woody detritus, despite its importance, is often overlooked in forest ecosystems leading to uncertainties regarding its dynamics [33]. High concentrations of slowly decomposing lignin in woody litter can lead to sigmoid patterns in mass loss, which become more pronounced as the size of the decomposing woody litter increases [36].

ROLE OF WOOD-DECAY FUNGI IN WOOD LITTER DECOMPOSITION

Woody litter decomposition is linked to biodiversity, as it determines the quality of the woody litter inhabited by many organisms [36]. It is broken down mainly through microbial activity, physical weathering, leaching, and the activity of faunal organisms [24, 43]. However, microorganisms are the most essential factor in decomposition. This process is primarily carried out by fungi, which are capable of producing specific enzymes, and their hyphae provide access to new substrates [2, 51–54], while bacteria play a comparatively minor direct role in breaking down natural lignocellulose complexes. However, bacteria can modify and decompose lignin derivatives, particularly under conditions unfavorable to fungal activity, such as anoxic environments. Decomposer fungi compete with bacteria for labile carbon sources, but environmental factors such as pH and soil moisture influence which group dominates the decomposition process. Generally, fungi perform better under acidic and relatively dry environmental conditions [2, 55]. Multi-species litter mixtures have lower bacterial diversity, higher microbial biomass, and fungal diversity than single-species litter mixtures [56].

Coarse woody litter is a primary source of decay material and energy for decomposer fungi in forests. Based on the capabilities of different fungal species to decompose lignocellulose, wood decomposition by fungi is categorized into three distinct decay types: 1) white-rot, 2) brown-rot, and 3) soft-rot [8]. The extracellular enzymes fungi produce play a central role in transforming and mineralizing coarse woody debris during this process. They are critical in facilitating energy flow to higher trophic levels [13]. Fungi alter the colour of wood during decomposition and cause changes in microscopic traits, decayed wood colour, and corresponding loss of acid nonhydrolyzable residue (AUR) and holocellulose [57]. In addition to releasing energy and nutrients, organisms living on wood in terrestrial and stream ecosystems fix significant amounts of nitrogen [24] and significantly impact carbon storage in forest ecosystems [58].

ROLE OF ASCOMYCETES IN WOODY LITTER DECOMPOSITION

The natural structure of forests provides varying microclimatic conditions and dynamics that fulfil the requirements of wood-decomposing fungi [54]. Ascomycetes, basidiomycetes, deuteromycetes, and certain types of mucoraceous species, have been isolated from wood [59, 60]. Their effects on this substrate vary, partly attributable to their nutrient acquisition strategies [61]. In the last decades, the development and use of quantitative methods have revealed that fungi have an important role in plant litter decomposition, significantly transferring energy and nutrients to higher trophic levels [62]. In evolutionary ecology, woody vegetation and xylotrophic fungi play a crucial role

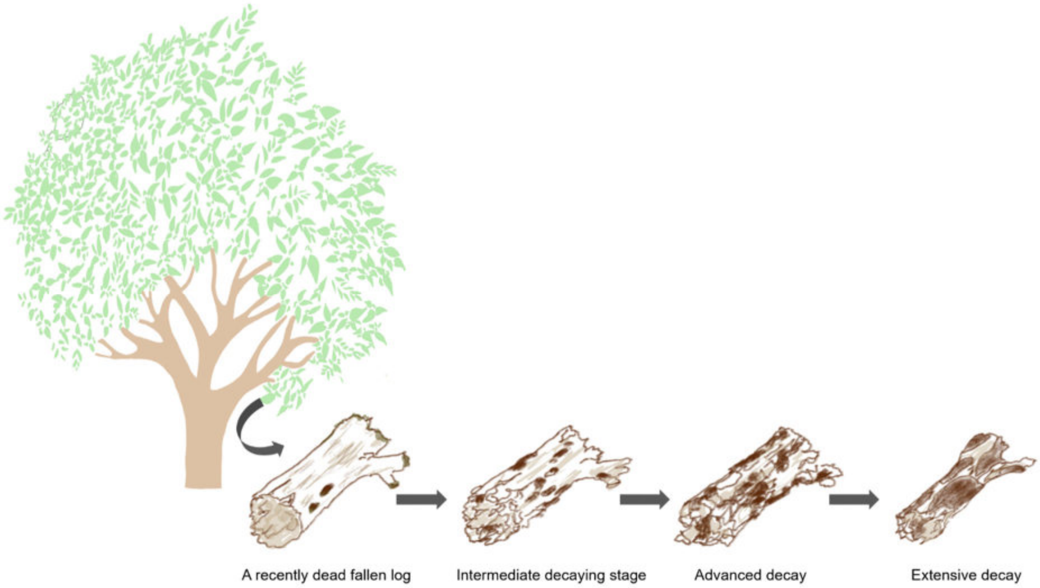

Fig. 3 The succession of the log decomposition (adapted from Müller-Using and Bartsch [32]).

in forest systems. Xylotrophic fungi are an obligatory component of woody vegetation [63].

Ascomycetes are characterized by a sac-like structure called an ascus, which contains spores. They are incredibly diverse, with species occupying various ecological niches, including wood litter [59]. One of the intriguing aspects of these fungi is their adaptability and resilience, and their wide distribution speaks volumes about their ecological versatility and their ability to thrive in different environmental conditions [64]. In addition to their ecological position, ascomycetes possess diverse enzyme complexes for lignocellulose degradation. Key dynamic carbohydrate enzymes (CAZymes), such as glycoside hydrolases (GHs), carbohydrate esterases (CEs), lytic polysaccharide monooxygenases (LPMOs), and accessory activity enzymes (AA) that include laccases and non-specific peroxygenases, are generated by genomic and transcriptional studies. Ascomycetes hold a discrete complement of lignocellulolytic enzymes, allowing them to destroy cellulose and hemicellulose, and alter lignin through oxidative mechanisms [40, 65, 66]. Their metabolic approach was less contingent on ligninolysis compared to basidiomycetes. They adapted to early decomposition stages and stress-prone habitats [67]. This underscores the matching roles of ascomycetes and basidiomycetes in wood litter deterioration and highlights the need for additional functional studies on ascomycete-driven decomposition.

Ascomycetes are essential from the ecological point of view and represent the most prevalent fungal taxa in freshwater environments [62, 68, 69]. According to the occurrence, ascomycetes can be classified into 1) freshwater ascomycetes, 2) freshwater and terrestrial ascomycetes, 3) freshwater and marine ascomycetes, and 4) generalist ascomycetes (found in all ecosystems) [69, 70].

While other groups of fungi like basidiomycetes are often associated with wood decay and broadly studied, ascomycetes' role should not be underestimated. Developing evidence recommends that ascomycetes perform a key part in the early stages of wood decomposition, particularly under dry or stressful situations when basidiomycetes are less dynamic [40, 71]. Many ascomycetes depend on a more oxidative and less ligninolytic approach than basidiomycetes, specializing in ligninolysis. This enables them to thrive in nutrient-poor or arid conditions [67]. This group of fungi are efficient decomposers of wood litter and can even degrade lignin, a complex organic polymer that most other fungi cannot process [53]. Understanding the diversity and role of ascomycetes in wood litter decomposition is therefore essential for a comprehensive understanding of nutrient cycling in forest ecosystems. However, despite the wealth of information available, there are still many unanswered questions about the diversity of wood litter-inhabiting ascomycetes. Future studies should strive to address these gaps, providing a broader understanding of these crucial organisms and their role in forest ecosystems. In conclusion, the diversity of wood litter-inhabiting ascomycetes is a testament to the complexity and resilience of forest ecosystems. Understanding this diversity and its implications for forest health and productivity is an important area of research, with potential applications in forest management and conservation.

HOST-RECURRENCE AND -EXCLUSIVITY

“That which one prefers; the object of prior choice the favorite” has been termed as “host-preference” [72]. It is a concept that has frequently been applied in mycology to show a common or unique fungus occurrence on a specific host in comparison to other hosts [73–75]. This term was initially offered by plant pathologists [76]. Zhou and Hyde [77], suggested “host-recurrence” and “host-exclusivity” as suitable terms for fungal use instead of host-preference. Furthermore, they stated that host-recurrence is an appropriate term with regard to saprobic fungi. Host specificity is regulated by the genetic composition of both the parasite and the host, which together influence the dynamics and outcome of their interaction [77]. Subsequently, Mukwevho et al [78] incorporated these concepts to describe host-exclusivity and host-recurrence in saprobic fungi. Host-exclusivity refers to fungi that grow on material derived from a specific host or a limited range of closely related hosts, whereas host-recurrence is defined as fungi that mainly grow on material from a particular host but may also colonize material from other hosts within the same habitat. Comprehensive documentation of fungal host associations and geographic distributions is vital for advancing the understanding of fungal biology and their ecological interactions [60].

Many microfungal species in decomposing leaves are recurrent on a specific host and at specific stages of decay [79]. Tennakoon et al [80], evidenced host-specificity in a high number of species isolated from dead leaves. Wood inhabiting ascomycetes had diverse levels of host preference in temperate regions [81]. Host-recurrence of palm fungi was demonstrated in various taxa [82–84]. However, it seems that strong host-recurrence is rare among wood-dwelling fungi, whereas their habitat and substrata characters are substantial in this group [85].

DEVELOPMENTS AND FINDINGS (GLOBAL SCENARIO OF WOOD LITTER-INHABITING ASCOMYCETES)

As previously stated, litter decomposition serves as a vital indicator of the ecosystem’s health as it facilitates the return of plant carbon (C), nitrogen (N), and phosphorus (P) back into the soil and atmosphere, alongside other essential nutrients. Recent research has provided new insights into the role of ascomycetes in wood litter decomposition.

Biodiversity and distribution

The biodiversity of wood litter-inhabiting ascomycetes is remarkable. They are estimated to include almost 100,000 species, and this diversity is continually expanding as new species are discovered [86–88]. Wood litter-inhabiting ascomycetes are found in various habitats, from temperate to tropical forests and aquatic environments [59, 70]. As woody plants are persistent and some of them provide broad surface areas for the colonization of saprobic microfungi, they seem to have a rich diversity of fungi [89]. Wooden tissues inhabiting endophytic fungi frequently appear as primary wood-decaying fungi on dead wood substrates [90–92]. The number of species of both basidiomycetes and ascomycetes in fine woody debris is significantly higher than in coarse woody debris. Fine wood litter is essential for the wood-dwelling fungi diversity, particularly ascomycetes, in temperate broad-leaf forests. However, for the occurrence of numerous basidiomycete species, coarse woody debris is also required [54].

Management factors such as forest history, continuity and availability of deadwood, and habitat fragmentation can affect fungal diversity patterns along geographical gradients. Increased deadwood in forest ecosystems can increase diversity [93]. Meier et al [94] found remarkable diversity in the composition of fungal communities across the elevation gradient, nevertheless, the richness of fungi did not undergo significant alteration with this factor, which is significantly different from the criterion observed for other taxa over this elevation gradient and others. This high level of biodiversity indicates the ecological versatility of these fungi and their ability to colonize diverse substrates. Freshwater ascomycetes exhibit a preference for colonizing woody litter [95]. Marine fungi distribution is primarily influenced by factors such as water temperature and salinity [96].

Biotechnological applications

Compared to other biological sources, especially plants, fungi offer significant advantages. They play pivotal roles in various biotechnological applications and hold great potential for industrial exploitation due to their metabolic diversity, ease of cultivation in large-scale bioreactors, and genetic tractability [97]. Fungi and their value-added products have diverse biotechnological applications across agriculture, healthcare, industrial processes, and environmental management. In particular, fungal enzymes such as xylanases, cellulases, lipases, phytases, proteases, and amylases play key roles in these sectors [98]. Pimpisai et al [99] assessed the co-culturing approach of enzyme-producing saccharolytic molds (*Aspergillus oryzae* TISTR 3086 and *Amylomyces rouxii* TISTR 3182) with *Saccharomyces cerevisiae* TISTR 5088 to enhance bioethanol production from cassava starch.

Among wood decomposer fungi, white rot and brown rot fungi, along with their enzymes, are increasingly utilized in a wide range of biotechnological applications, including pulping, Pitch removal, textile treatment, lignin modification to enhance inter-fiber bonding, pretreatment processes for ethanol production and improved wood permeability, treatment of waste effluents and bioremediation, as well as biochelation and recycling of treated wood [100]. In contrast, soft rot fungi have found more limited applications in biotechnology. However, some species, like *Trichoderma reesei*, have played important roles in enzyme production and are recognized as valuable sources of cellulase [101].

Ecological role

Wood litter-inhabiting ascomycetes are integral to the health and sustainability of forest ecosystems. They are primary decomposers, breaking down complex organic materials in deadwood into simpler compounds [52, 53]. This process of decomposition not only recycles nutrients back into the soil, enhancing its fertility but also contributes to carbon sequestration [102, 103]. By storing carbon in their mycelial networks, these fungi help mitigate the impacts of climate change. Different fungal species inhabiting wood litter exhibit different capacities of decomposition [53, 104].

As pointed out, decomposer fungi are typically categorized into three stages based on the type of decay they cause: white rots, brown rots, and soft rots. The rot is identified by a gradual reduction in the thickness of the cell walls. Brown-rot fungi primarily decompose cellulose and hemicellulose polymers in wood and can adapt to lignin [105]. Soft rot is mainly caused by a wide range of ascomycetes and deuteromycetes, often referred to as "microfungi" in that they do not generally form large fruiting bodies such as those characteristics commonly associated with many brown and white rot fungi [61, 106]. Soft-rot fungi, which grow inside the cell walls, are the main wood-decaying fungi containing a significant amount of water [107]. Degradation of lignin is done by white-rot fungi (particularly basidiomycetes in *Agaricomycotina*) [40], however, some ascomycete taxa (species of *Xylariales*) have the potential to degrade lignin [53, 108].

Cornwell et al [43] found that species diversity is more important than climate differences as a driver of decomposition rates and that a species' litter decomposability is consistently associated with its ecological strategy across diverse ecosystems globally. According to the authors, this represents a novel link between the carbon strategy of the whole plant and biogeochemical cycling. Increasing the richness of litter species can also increase the release of carbon and nitrogen [56].

Community dynamics

A group of species coexisting in a restricted time and area is called a community [109]. The "construction and maintenance of local communities through sequential arrival of potential colonists from an external species pool" has been characterized as community assembly [110]. The dynamics within the communities of fungi that colonize wood are heavily influenced by abiotic factors, such as moisture, temperature, and oxygen level, as well as biotic factors like fungal succession and competition [71, 111]. As deadwood is a dynamic substrate, the physical and chemical microenvironment undergoes continuous changes during its decomposition. To adapt to these fluctuations, wood-dwelling fungi have developed various strategies for dispersal, establishment, competition, and resilience against both biotic and abiotic stress [112].

Wood-inhabiting fungal communities comprise numerous decomposer species in the same substrate, therefore rendering them species-rich. These fungal species interact with each other because fungal community composition expands progressively [112]. The composition of wood-inhabiting fungal communities is dynamic undergoing changes over time. It often seems to be a progressive change from the first colonization step to the final stages of degradation [61]. Therefore, "fungal succession" refers to this time-related change of fungal communities during the decaying process [11, 113]. In this process, interactions between fungal species, have a substantial role in determining their success in colonizing and maintaining territory [114]. Some fungi also excrete compounds that directly impact the growth and evolvement of other fungal taxa [115].

Rayner and Todd [61], recommended the study of community structure and dynamics of fungi in decaying wood should encompass both spatial and temporal dimensions. They emphasized prioritizing the examination of community structure and development over a narrow focus solely on succession. In theory, direct interaction (contact between mycelia) or indirect mechanisms, could result in both deadlock and replacement phenomena. Some indirect mechanisms that can lead to deadlock or replacement in wood include nutrient reflects, production of antibiotics, removal of toxic materials, host resistance removal, and incidental environmental factors [61].

As wood decomposes, its physical and chemical properties alter, creating different ecological niches. The chemical constituents of the wood undergo substantial changes. Cellulose and hemicellulose are the first to be broken down into more resistant lignin, which favors the growth of fungal taxa adept at lignin degradation [111, 116]. During decomposition, these changes are directly linked to the alteration in the mosaic of fungal enzymes and the ever-changing fungal community from innovator colonizing ascomycetes to more dedicated basidiomycetes [71, 111]. These structural and functional variations have been elucidated by more recent metagenomic and metatranscriptomic analyses where fungal genes responsible for the degradation of lignocellulose and temporal changes in community residence were tracked [117, 118].

With advancements in molecular biology techniques, many novel species of ascomycetes have been discovered. These discoveries have expanded our understanding of the diversity and their roles in various ecosystems. For instance, a research topic aimed to discover more novel species of ascomycetes focusing on their taxonomy and phylogeny, as well as the genetic and molecular characterization of these fungi and their interaction with the host species. These novel species could potentially have significant impacts on wood litter decomposition. However, further research is needed to fully understand these impacts.

METHODS FOR ASSESSING THE DIVERSITY OF MICROFUNGI FROM WOODY LITTER

Various methods have been applied to estimate the diversity of litter fungi, among them the culture-based approach is the most frequently used method [119–123]. Traditionally, culture-based methods combined with phylogenetic studies have been used in fungal diversity studies worldwide [59, 124]. First, this polyphasic approach used only morphological characteristics, physiological and biochemical traits, or responses to chemical tests to differentiate fungal taxa [125]. However, with the development of molecular methods and DNA sequencing, traditional methods have been used in combination with evolutionary analyses [124, 126–128]. These methods have revealed fungal taxa up to the species level [129]. Moreover, it can identify diversity patterns, and resource utilization while determining the fungal community composition [130]. Nonetheless, relying solely on traditional phylogeny and culture-based studies to understand fungal species distribution poses challenges due to difficulties in isolating slow-growing and weakly competitive species for complete culture-based assays [129].

High throughput sequencing (HTS) technologies led to a better understanding of microorganisms' ecology, diversity, and distribution patterns [87, 131, 132]. The first HTS platform commercially became available in 2005 and utilized emulsion polymerase chain reaction (PCR) for parallel template amplification [133]. The sequence length, accuracy, and analysis of these methods have been considerably modified, and Illumina MiSeq and Ion Torrent platforms have been selective methods for researchers [134]. The possibility of analyzing the diversity of fungal species in species-rich ecosystems has been facilitated by HTS [135]. HTS supports recovering fungi that cannot be cultured, specifically inhabit extreme environmental conditions [136]. Thus, HTS has the potential to unveil fungal diversity, encompassing cryptic and non-cultivable fungi, such as *Archaeorhizomycetes*, *Cryptomycota*, and *Zygomycotina*, and non-cultivable symbiotic fungi like mycorrhizal and nematophagous fungi [17, 137, 138].

Several studies have been conducted in different types of forests using amplicon-based metagenomics. For instance, Ovaskainen et al [139] identified wood-dwelling fungi with 454 sequencing data in a protected semi-natural spruce-dominated forest in the north of Helsinki, Finland. Kubartová and coworkers [140] surveyed fungal communities by 454 sequencing in decaying logs of Norway spruce at different spatial scales at two different locations in Sweden. Yamashita et al [141] evaluated the correlation between the decomposition rate of coarse woody debris and the fungal community that was identified by HTS in a deciduous broad-leaved forest in Japan. Runnel et al [142] identified wood-inhabiting fungi with Illumina HTS and compared it with polypores' fruiting bodies in a wetland pine forests in Estonian. Hoppe et al [130] studied the community structure and richness of fungal in Norway spruce and European beech woody litter using 454 pyrosequencing in temperate forests in the UNESCO Biosphere Reserve "Schwäbische Alb" in southwestern Germany. Vaz et al [143] surveyed the diversity of fungi associated with wood using HTS in tropical forests. Ritter et al [135] used HTS of DNA of fungi that existed in the soil and organic litter for surveying the impact of soil features, habitat, and sites in Amazonia. Therefore, the combination of culture-based methods with high-resolution culture-independent methods such as HTS has been used to assess the fungal diversity from the most diverse environments [129, 144].

CONCLUSION AND FUTURE PERSPECTIVES

This review paper provides an overview of ascomycetes, focusing on their diversity and role in wood litter decomposition. We delve into the basic concepts related to these fungi and the wood litter they inhabit, highlighting their remarkable diversity. Further, we explore the significant contribution they make to wood litter decomposition, comparing their role with other fungi like basidiomycetes. The paper also highlights recent developments and findings in the field, including the discovery of novel species and their potential impact.

Despite the considerable progress in understanding the role of ascomycetes in wood litter decomposition, several gaps remain in our current knowledge. For instance, there is a limited number of comprehensive investigations into the systematics of fungal species associated with woody litter [145–148]. Furthermore, our understanding of how the diversity of ascomycetes influences the rate and extent of wood litter decomposition is still incomplete. Another major gap lies in our understanding of how environmental changes impact fungi and their role in wood litter decomposition. Research indicates that fungi classified as ascomycetes, show sensitivity to environmental changes [149]. However, the specific impacts of these changes and their role in wood litter decomposition are not well understood.

Given these gaps, future research should focus on several key areas. Firstly, more comprehensive studies are needed to understand the taxonomic systematics of ascomycetes in wood litter. This could involve exploring uncharted regions and habitats, as well as employing advanced molecular biology techniques to discover novel species. Secondly, research should aim to elucidate how the diversity of ascomycetes influences wood litter decomposition. This could involve experimental studies manipulating the diversity of ascomycetes and observing the impacts on wood litter decomposition. Lastly, there is a pressing need to understand how environmental changes impact fungi and their role in wood litter decomposition. This could involve long-term monitoring studies to track changes in ascomycete communities and wood litter decomposition rates under changing environmental conditions.

Acknowledgements: Naghmeh Afshari is grateful for the Chiang Mai University Presidential Scholarship 2020 and partial support from Prof. Saisamorn Lumyong. Naghmeh Afshari also thanks Mae Fah Luang University for the research collaboration. Furthermore, she would like to thank Miss Mona Afshari for her help to draw Figure 3. Kevin D. Hyde and Fatimah Alotibi thank the ongoing Research Funding Program (ORF-2025-114) at King Saud University, Riyadh, Saudi Arabia. Chitrabhanu S. Bhunjun would like to thank the National Research Council of Thailand (NRCT) grant "Total fungal diversity in a given forest area with implications towards species numbers, chemical diversity, and biotechnology" (grant no. N42A650547) and Mae Fah Luang University for the basic research scholar 2567 grant (grant no. 671A05003). Antonio R. Gomes de Farias collaborated on this work while he was affiliated with the Center of Excellence in Fungal Research. Maryam T. Noorabadi would like to thank the National Natural Science Foundation of China (Nos. 32370021 and 31860008), the Innovative Team Program of the Department of Education of Guangdong Province (Nos. 2022KCXTD015 and 2022ZDJS020), and the Project of Fungi Investigation in the Tomur Mountains National Nature Reserve for their support.

REFERENCES

1. Treseder KK, Lennon JT (2015) Fungal traits that drive ecosystem dynamics on land. *Microbiol Mol Biol Rev* **79**, 243–262.
2. Bani A, Pioli S, Ventura M, Panzacchi P, Borruso L, Tognetti R, Tonon G, Brusetti L (2018) The role of microbial community in the decomposition of leaf litter and deadwood. *Appl Soil Ecol* **126**, 75–84.
3. Sayer EJ, Rodtassana C, Sheldrake M, Bréchet LM, Ashford OS, Lopez-Sangil L, Kerdraon-Byrne D, Castro B, et al (2020) Revisiting nutrient cycling by litterfall – Insights from 15 years of litter manipulation in old-growth lowland tropical forest. *Adv Ecol Res* **62**, 173–223.
4. Cromack K, Todd RL, Monk CD (1975) Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol Biochem* **7**, 265–268.
5. Rayner ADM, Boddy L (1988) *Fungal Decomposition of Wood: Its Biology and Ecology*, Amoebae and myxomycetes. John Wiley & Sons, Chichester, pp 132–134.
6. Barron GL (2003) Predatory fungi, wood decay, and the carbon cycle. *Biodivers* **4**, 3–9.
7. Rousk J, Brookes PC, Bååth E (2009) Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Appl Environ Microbiol* **75**, 1589–1596.
8. Fukasawa Y (2012) Effects of wood decomposer fungi on tree seedling establishment on coarse woody debris. *Forest Ecol Manag* **266**, 232–238.
9. Johnson D, Vandenkoornhuyse PJ, Leake JR, Gilbert L, Booth RE, Grime JP, Young JPW, Read DJ (2004) Plant communities affect arbuscular mycorrhizal fungal diversity and community composition in grassland microcosms. *New Phytol* **161**, 503–515.
10. Abrego N, Salcedo I (2013) Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: is it a question of quantity or quality? *Forest Ecol Manag* **291**, 377–385.
11. Tennakoon DS, Gentekaki E, Jeewon R, Kuo CH, Promputtha I, Hyde KD (2021) Life in leaf litter: Fungal community succession during decomposition. *Mycosphere* **12**, 406–429.
12. Allison SD, Vitousek PM (2004) Extracellular enzyme activities and carbon chemistry as drivers of tropical plant litter decomposition. *Biotropica* **36**, 285–296.
13. Simonis JL, Raja HA, Shearer CA (2008) Extracellular enzymes and soft rot decay: Are ascomycetes important degraders in freshwater. *Fungal Divers* **31**, 135–146.
14. Mapook A, Hyde KD, Hassan K, Kemkuignou BM, Čmoková A, Surup F, Kuhnert E, Paomephan P, et al (2022) Ten decadal advances in fungal biology leading towards human well-being. *Fungal Divers* **116**, 547–614.
15. Fukasawa Y, Tateno O, Hagiwara Y, Hirose D, Osono T (2012) Fungal succession and decomposition of beech cupule litter. *Ecol Res* **27**, 735–743.
16. Sridhar KR, Karamchand KS, Hyde KD (2010) Wood-inhabiting filamentous fungi in 12 high-altitude streams of the Western Ghats by damp incubation and bubble chamber incubation. *Mycoscience* **51**, 104–115.
17. Blackwell M (2011) The Fungi: 1, 2, 3 ... 5.1 million species?. *Am J Bot* **98**, 426–438.
18. Woldendorp G, Keenan RJ (2005) Coarse woody debris in Australian forest ecosystems: A review. *Austral Ecol* **30**, 834–843.
19. Berg B, McClaugherty C (2008) *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*, Springer, Berlin.
20. Ruprecht E, Jozsa J, Ölvedi TB, Simon J (2010) Differential effects of several "litter" types on the germination of dry grassland species. *J Veg Sci* **21**, 1069–1081.
21. Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in Terrestrial Ecosystems*, University of California Press, Berkeley, CA.
22. Facelli JM, Pickett ST (1991) Plant litter: its dynamics and effects on plant community structure. *Bot Rev* **57**, 1–32.
23. Bremer E, Van Houtum W, Van Kessel C (1991) Carbon dioxide evolution from wheat and lentil residues as affected by grinding, added nitrogen, and the absence of soil. *Biol Fertil Soils* **11**, 221–227.
24. Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory

SV, Lattin JD, Anderson NH, Cline SP, et al (1986) Ecology of coarse woody debris in temperate ecosystems. *Adv Ecol Res* **15**, 133–302.

25. Zimmer M (2019) Detritus. In: *Encyclopedia of Ecology*, Elsevier, Amsterdam, pp 292–301.
26. Tritton LM (1980) *Dead Wood in the Northern Hardwood Forest Ecosystem*, Yale University, New Haven, CT, USA.
27. Wei X, Kimmins JP, Peel K, Steen O (1997) Mass and nutrients in woody debris in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. *Can J For Res* **27**, 148–155.
28. Eaton JM, Lawrence D (2009) Loss of carbon sequestration potential after several decades of shifting cultivation in the Southern Yucatán. *Forest Ecol Manag* **258**, 949–958.
29. Franklin JF SH, Harmon ME (1987) Tree death as an ecological process: the causes, consequences, and variability of tree mortality. *BioScience* **37**, 550–556.
30. Abbott DT, Crossley Jr DA (1982) Woody litter decomposition following clear-cutting. *Ecology* **63**, 35–42.
31. Christensen M, Hahn K, Mountford EP, Ódor P, Standovár T, Rozenbergar D, Diaci J, Wijdeven S, et al (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecol Manag* **210**, 267–282.
32. Müller-Using S, Bartsch N (2009) Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. *Eur J For Res* **128**, 287–296.
33. Song Z, Dunn C, Lü XT, Qiao L, Pang JP, Tang JW (2017) Coarse woody decay rates vary by physical position in tropical seasonal rainforests of SW China. *Forest Ecol Manag* **385**, 206–213.
34. Yan E, Wang X, Huang J (2006) Concept and classification of coarse woody debris in forest ecosystems. *Front Biol China* **1**, 76–84.
35. Kappes H, Catalano C, Topp W (2007) Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. *Appl Soil Ecol* **36**, 190–198.
36. Tuomi M, Laiho R, Repo A, Liski J (2011) Wood decomposition model for boreal forests. *Ecol Modell* **222**, 709–718.
37. Xiong S, Nilsson C (1999) The effects of plant litter on vegetation: A meta-analysis. *J Ecol* **87**, 984–994.
38. Prescott CE (2010) Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochem* **101**, 133–149.
39. Cornelissen JH, Van Bodegom PM, Aerts R, Callaghan TV, Van Logtestijn RS, Alatalo J, Stuart Chapin F, Gerdol R et al (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecol Lett* **10**, 619–627.
40. Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, et al (2012) The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336**, 1715–1719.
41. Donath TW, Eckstein RL (2010) Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. *Plant Ecol* **207**, 257–268.
42. Hoorens B, Coomes D, Aerts R (2010) Neighbour identity hardly affects litter-mixture effects on decomposition rates of New Zealand forest species. *Oecologia* **162**, 479–489.
43. Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, et al (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol Lett* **11**, 1065–1071.
44. Wardle DA, Nilsson MC, Zackrisson O, Gallet C (2003) Determinants of litter mixing effects in a Swedish boreal forest. *Soil Biol Biochem* **35**, 827–835.
45. Freschet GT, Aerts R, Cornelissen JH (2012) A plant economics spectrum of litter decomposability. *Funct Ecol* **26**, 56–65.
46. Preston CM, Nault JR, Trofymow JA (2009) Chemical changes during 6 years of decomposition of 11 litters in some Canadian forest sites. Part 2. ^{13}C abundance, solid-state ^{13}C NMR spectroscopy and the meaning of "lignin". *Ecosystems* **12**, 1078–1102.
47. Koorem K, Price JN, Moora M (2011) Species-specific effects of woody litter on seedling emergence and growth of herbaceous plants. *PLoS One* **6**, e26505.
48. Giweta M (2020) Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: A review. *J Ecol Environ* **44**, 11.
49. Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, et al (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J Ecol* **101**, 943–952.
50. Onega TL, Eickmeier WG (1991) Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. *Bull Torrey Bot Club* **118**, 52–57.
51. Leifheit EF, Verbruggen E, Rillig MC (2015) Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation. *Soil Biol Biochem* **81**, 323–328.
52. Bucher VVC, Hyde KD, Pointing SB, Reddy CA (2004) Production of wood decay enzymes, loss of mass, and lignin solubilization in wood by diverse tropical freshwater fungi. *Fungal Divers* **15**, 1–14.
53. Pointing SB, Pelling AL, Smith GJD, Hyde KD, Reddy CA (2005) Screening of basidiomycetes and xylariaceous fungi for lignin peroxidase and laccase gene-specific sequences. *Mycol Res* **109**, 115–124.
54. Nordén B, Götmark F, Tönnberg M, Ryberg M (2004) Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. *Forest Ecol Manag* **194**, 235–248.
55. Van der Wal A, Geydan TD, Kuyper TW, De Boer W (2013) A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiol Rev* **37**, 477–494.
56. Santonja M, Rancon A, Fromin N, Baldy V, Hättenschwiler S, Fernandez C, Montès N, Mirleau P (2017) Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland. *Soil Biol Biochem* **111**, 124–134.
57. Fukasawa Y, Osono T, Takeda H (2009) Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. *J Forest Res* **14**, 20–29.
58. Yatskov M, Harmon ME, Krankina ON (2003) A

chronosequence of wood decomposition in the boreal forests of Russia. *Can J Forest Res* **33**, 1211–1226.

59. Hyde KD, Bussaban B, Paulus B, Crous PW, Lee S, McKenzie EH, Photita W, Lumyong S (2007) Diversity of saprobic microfungi. *Biodivers Conserv* **16**, 7–35.
60. De Silva NI, Hyde KD, Lumyong S, Phillips AJL, Bhat DJ, Maharachchikumbura SSN, Thambugala KM, Tennakoon DS, et al (2022) Morphology, phylogeny, host association and geography of fungi associated with plants of *Annonaceae*, *Apocynaceae* and *Magnoliaceae*. *Fungal Divers* **113**, 955–1076.
61. Rayner AD, Todd NK (1980) Population and community structure and dynamics of fungi in decaying wood. *Adv Bot Res* **7**,333–420.
62. Gulis V, Suberkropp K, Rosemond AD (2008) Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. *Appl Environ Microbiol* **74**, 1094–1101.
63. Blinkova O, Ivanenko O (2018) Communities of woody vegetation and wood destroying fungi in natural and semi-natural forests of Kyiv city, Ukraine. *Cent Eur For J* **64**, 55–66.
64. Senanayake IC, Pem D, Rathnayaka AR, Wijesinghe SN, Tibpromma S, Wanasinghe DN, Phookamsak R, Kularathnage ND, et al (2022) Predicting global numbers of teleomorphic ascomycetes. *Fungal Divers* **114**, 237–278.
65. Riley R, Salamov AA, Brown DW, Nagy LG, Floudas D, Held BW, Levasseur A, Lombard V, et al (2014) Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc Natl Acad Sci USA* **111**, 9923–9928.
66. Ruiz-Duenas FJ, Lundell T, Floudas D, Nagy LG, Barrasa JM, Hibbett DS, Martínez AT (2013) Lignin-degrading peroxidases in *Polyporales*: an evolutionary survey based on 10 sequenced genomes. *Mycologia* **105**, 1428–1444.
67. Presley GN, Panisko E, Purvine SO, Schilling JS (2018) Coupling secretomics with enzyme activities to compare the temporal processes of wood metabolism among white and brown rot fungi. *Appl Environ Microbiol* **84**, e00159-18.
68. Calabon MS, Hyde KD, Jones EBG, Luo ZL, Dong W, Hurdeal VG, Gentekaki E, Rossi W, et al (2022) Freshwater fungal numbers. *Fungal Divers* **114**, 3–235.
69. Calabon MS, Hyde KD, Jones EBG, Bao DF, Bhunjun CS, Phukhamsakda C, Shen HW, Gentekaki E, et al (2023) Freshwater fungal biology. *Mycosphere* **14**, 195–413.
70. Vijaykrishna D, Hyde KD (2006) Inter-and intra-stream variation of lignicolous freshwater fungi in tropical Australia. *Fungal Divers* **21**, 203–224.
71. Baldrian P (2017) Forest microbiome: diversity, complexity and dynamics. *FEMS Microbiol Rev* **41**, 109–130.
72. Simpson JA, Weiner ESC (1989) *The Oxford English Dictionary*, Clarendon Press, Oxford.
73. Hughes SJ (1981) New Zealand fungi: 31. *Capnobotrys*, an anamorph of Metacapnodiaceae. *N Z J Bot* **19**, 193–226.
74. Malvick DK, Grau CR, Percich JA (1998) Characterization of *Aphanomyces euteiches* strains based on pathogenicity tests and random amplified polymorphic DNA analyses. *Mycol Res* **102**, 465–475.
75. Augustin C, Ulrich K, Ward E, Werner A (1999) RAPD-based inter- and intra-varietal classification of fungi of the *Gaeumannomyces-Phialophora* complex. *J Phytopathol* **147**, 109–117.
76. Rapilly F (1998) Pathogen resistance of plants: historical evolution of concepts. *Cah Agricult* **7**, 223–228.
77. Zhou D, Hyde KD (2001) Host-specificity, host-exclusivity, and host-recurrence in saprobic fungi. *Mycol Res* **105**, 1449–1457.
78. Mukwevho VO, Dreyer LL, Roets F (2020) Interplay between differential competition and actions of spore-vectors explain host exclusivity of saprobic fungi in Protea flowers. *Antonie van Leeuwenhoek* **113**, 2187–2200.
79. Santana ME, Lodge DJ, Lebow P (2005) Relationship of host recurrence in fungi to rates of tropical leaf decomposition. *Pedobiologia* **49**, 549–564.
80. Tennakoon DS, Kuo CH, Purahong W, Gentekaki E, Pumas C, Promputtha I, Hyde KD (2022) Fungal community succession on decomposing leaf litter across five phylogenetically related tree species in a subtropical forest. *Fungal Divers* **115**, 73–103.
81. Huhndorf SM, Lodge DJ (1997) Host specificity among wood-inhabiting pyrenomycetes (Fungi, Ascomycetes) in a wet tropical forest in Puerto Rico. *Trop Ecol* **38**, 307–315.
82. Hyde KD (1992) Fungi from palms I. The genus *Linocarpon*, a revision. *Sydowia* **47**, 32–54.
83. Hyde KD (1994) Fungi from palms. XIII. The genus *Oxydothis*, a revision. *Sydowia* **46**, 265–314.
84. Hyde KD (1995) Fungi from palms XXII. A new species of *Ascotaiwania*. *Sydowia* **47**, 213–216.
85. Lodge DJ (1997) Factors related to diversity of decomposer fungi in tropical forests. *Biodivers Conserv* **6**, 681–688.
86. Bhunjun CS, Niskanen T, Suwannarach N, Wannathes N, Chen YJ, McKenzie EH, Maharachchikumbura SS, Buyck B, et al (2022) The numbers of fungi: Are the most speciose genera truly diverse?. *Fungal Divers* **114**, 387–462.
87. Phukhamsakda C, Nilsson RH, Bhunjun CS, de Farias AR, Sun YR, Wijesinghe SN, Raza M, Bao DF, et al (2022) The numbers of fungi: Contributions from traditional taxonomic studies and challenges of metabarcoding. *Fungal Divers* **114**, 327–386.
88. Hyde KD, Amuhenage TB, Apurillo CCS, Asghari R, Aumentado HD, Bahkali AH, Bera I, Bhunjun CS, et al (2023) Fungalpedia, an illustrated compendium for the fungi and fungus-like taxa. *Mycosphere* **14**, 1835–1959.
89. Wong MKM, Hyde KD (2001) Diversity of fungi on six species of Gramineae and one species of Cyperaceae in Hong Kong. *Mycol Res* **105**, 1485–1491.
90. Promputtha I, Hyde KD, McKenzie EHC, Peberdy JF, Lumyong S (2010) Can leaf degrading enzymes provide evidence that endophytic fungi becoming saprobes? *Fungal Divers* **41**, 89–99.
91. Boddy L, Rayner ADM (1983) Mycelial interactions, morphogenesis and ecology of *Phlebia radiata* and *P. rufa* from oak. *Trans Br Mycol Soc* **80**, 437–448.
92. Parfitt D, Hunt J, Dockrell D, Rogers HJ, Boddy L (2010) Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecol* **3**, 338–346.
93. Ódor P, Heilmann-Clausen J, Christensen M, Aude E, van Dort KW, Piltaver A, Siller I, Veerkamp MT, et al (2006)

Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biol Conserv* **131**, 58–71.

94. Meier CL, Rapp J, Bowers RM, Silman M, Fierer N (2010) Fungal growth on a common wood substrate across a tropical elevation gradient: temperature sensitivity, community composition, and potential for above-ground decomposition. *Soil Biol Biochem* **42**, 1083–1090.
95. Shearer CA, Raja HA (2010) *Freshwater Ascomycetes Database*. Available at: http://fungi.life.illinois.edu/.
96. Hughes GC (1974) Geographical distribution of the higher marine fungi. *Veröff Inst Meeresforsch Bremerhaven* (Supp **5**), 419–441.
97. Hyde KD, Xu J, Rapior S, Jeewon R, Lumyong S, Niego AGT, Abeywickrama PD, Aluthmuhandiram JVS, et al (2019) The amazing potential of fungi: 50 ways we can exploit fungi industrially. *Fungal Divers* **97**, 1–136.
98. Kour D, Rana KL, Yadav N, Yadav AN, Singh J, Rastegari AA, Saxena AK (2019) Agriculturally and industrially important fungi: current developments and potential biotechnological applications. In: Yadav A, Singh S, Mishra S, Gupta A (eds) *Recent Advancement in White Biotechnology Through Fungi*, Fungal Biology, Springer, Cham., pp 1–64.
99. Pimpisai T, Maneerattanarungroj C, Kingkaew E, Ochaikul D (2024) Bioethanol production from cassava starch using co-culture of saccharolytic molds with *Saccharomyces cerevisiae* TISTR 5088. *ScienceAsia* **50**, ID 2024071.
100. Singh AP, Singh T (2014)) Biotechnological applications of wood-rotting fungi: A review. *Biomass Bioenergy* **62**, 198–206.
101. Li X-L, Dien BS, Cotta MA, Wu YV, Saha BC (2005) Profile of enzyme production by *Trichoderma reesei* grown on corn fiber fractions. In: Davison BH, Evans BR, Finkelstein M, McMillan JD (eds) *Twenty-Sixth Symposium on Biotechnology for Fuels and Chemicals*. ABAB Symposium. Humana Press, pp 321–334.
102. Wong MK, Goh TK, Hodgkiss IJ, Hyde KD, Ranghoo VM, Tsui CK, Ho WH, Wong WS, et al (1998) Role of fungi in freshwater ecosystems. *Biodivers Conserv* **7**, 1187–1206.
103. Gulis V, Su R, Kuehn KA (2019) Fungal decomposers in freshwater environments. In: Hurst C (ed) *The Structure and Function of Aquatic Microbial Communities*, Advances in Environmental Microbiology, vol 7, Springer, Cham., pp 121–155.
104. Valmaseda M, Almendros G, Martinez AT (1990) Substrate-dependent degradation patterns in the decay of wheat straw and beech wood by ligninolytic fungi. *Appl Microbiol Biotechnol* **33**, 481–484.
105. Krishna MP, Mohan M (2017) Litter decomposition in forest ecosystems: A review. *Energy Ecol Environ* **2**, 236–249.
106. Hatakka A, Hammel KE (2011) Fungal biodegradation of lignocelluloses. In: Hofrichter M (ed) *Industrial Applications*, The Mycota, vol 10, Springer, Berlin, Heidelberg, pp 319–340.
107. Stokland JN, Siitonen J, Jonsson BG (2012) *Biodiversity in Dead Wood*, Cambridge University Press, Cambridge.
108. Worrall JJ, Anagnost SE, Zabel RA (1997) Comparison of wood decay among diverse lignicolous fungi. *Mycologia* **89**, 199–219.
109. Morin PJ (2011) *Community Ecology*, 2nd (edn) Wiley-Blackwell, New Brunswick.
110. Fukami T (2010) Community assembly dynamics in space. In: Verhoef HA, Morin PJ (eds) *Community Ecology: Processes, Models, and Applications*, Oxford Academic, Oxford, pp 45–54.
111. Kahl T, Arnstadt T, Baber K, Bässler C, Bauhus J, Borken W, Buscot F, Floren A, et al (2017) Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *For Ecol Manage* **391**, 86–95.
112. Ottosson E (2013) *Succession of Wood-inhabiting Fungal Communities*, Swedish University of Agricultural Sciences, Uppsala, Sweden.
113. Dix NJ, Webster J (1995) *Fungal Ecology*, Chapman & Hall, London.
114. Boddy L, Hiscox J (2016) Fungal ecology: principles and mechanisms of colonization and competition by saprotrophic fungi. *Microbiol Spectr* **4**, 0019.
115. Shearer CA (1995) Fungal competition. *Can J Bot* **73**, 1259–1264.
116. Rajala T, Peltoniemi M, Pennanen T, Mäkipää R (2012) Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. *FEMS Microbiol Ecol* **81**, 494–505.
117. Žifčáková L, Větrovský T, Howe A, Baldrian P (2016) Microbial activity in forest soil reflects the changes in ecosystem properties between summer and winter. *Environ Microbiol* **18**, 288–301.
118. Johnston SR, Hiscox J, Savoury M, Boddy L, Weightman AJ (2019) Highly competitive fungi manipulate bacterial communities in decomposing beech wood (*Fagus sylvatica*). *FEMS Microbiol Ecol* **95**, fiy225.
119. Guo LD, Hyde KD, Liew ECY (2000) Identification of endophytic fungi from Livistona chinensis based on morphology and rDNA sequences. *New Phytol* **147**, 617–630.
120. Guo LD, Hyde KD, Liew ECY (2001) Detection and taxonomic placement of endophytic fungi within frond tissues of *Livistona chinensis* based on rDNA sequences. *Mol Phylogenet Evol* **20**, 1–13.
121. Guo LD, Huang GR, Wang Y, He WH, Zheng WH, Hyde KD (2003) Molecular identification of white morphotype strains of endophytic fungi from *Pinus tabulaeformis*. *Mycol Res* **107**, 680–688.
122. Parungao MM, Fryar SC, Hyde KD (2002) Diversity of fungi on rainforest litter in North Queensland, Australia. *Biodivers Conserv* **11**, 1185–1194.
123. Duong LM, Jeewon R, Lumyong S, Hyde KD (2006) DGGE coupled with ribosomal DNA gene phylogenies reveal uncharacterized fungal phylotypes. *Fungal Divers* **23**, 121–138.
124. Hyde KD, Jeewon R, Chen YJ, Bhunjun CS, Calabon MS, Jiang HB, Lin CG, Norphanphoun C, et al (2020) The numbers of fungi: Is the descriptive curve flattening? *Fungal Divers* **103**, 219–271.
125. Senanayake IC, Rathnayaka AR, Marasinghe DS, Calabon MS, Gentekaki E, Lee HB, Hurdeal VG, Pem D, et al (2020) Morphological approaches in studying fungi: collection, examination, isolation, sporulation and preservation. *Mycosphere* **11**, 2678–2754.
126. Phukhamsakda C, Hongsanan S, Ryberg M, Ariyawansa HA, Chomnunti P, Bahkali AH, Hyde KD (2016) The

evolution of *Massarineae* with *Longipedicellataceae* fam. nov. *Mycosphere* **7**, 1713–1731.

127. Hongsanan S, Maharachchikumbura SS, Hyde KD, Samarakoon MC, Jeewon R, Zhao Q, Al-Sadi AM, Bahkali AH (2017) An updated phylogeny of *Sordariomycetes* based on phylogenetic and molecular clock evidence. *Fungal Divers* **84**, 25–41.
128. Bhunjun CS, Phukhamsakda C, Jeewon R, Promputtha I, Hyde KD (2021) Integrating different lines of evidence to establish a novel ascomycete genus and family (*Anastomitrabeculia*, *Anastomitrabeculiaceae*) in *Pleosporales*. *J Fungi* **7**, 94.
129. Dissanayake A, Purahong W, Wubet T, Hyde K, Zhang W, Xu H, Zhang G, Fu C, et al (2018) Direct comparison of culture-dependent and culture-independent molecular approaches reveal the diversity of fungal endophytic communities in stems of grapevine (*Vitis vinifera*). *Fungal Divers* **90**, 85–107.
130. Hoppe B, Purahong W, Wubet T, Jurgen K, Bauhus T, Arnstadt T, Hofrichter M, Buscot F, Kruger D (2016) Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Divers* **77**, 367–379.
131. Zhou J, He Z, Deng Y, Tringe SG, Alvarez-Cohen L (2015) High-throughput metagenomic technologies for complex microbial community analysis: open and closed formats. *mBio* **6**, 02288-14.
132. Tedersoo L, Nilsson RH (2016) Molecular identification of fungi. In: Martin F (ed) *Molecular Mycorrhizal Symbiosis*, Wiley-Blackwell, London, pp 301–322.
133. Logares R, Haverkamp TH, Kumar S, Lanzén A, Nederbragt AJ, Quince C, Kauserud H (2012) Environmental microbiology through the lens of high-throughput DNA sequencing: synopsis of current platforms and bioinformatics approaches. *J Microbiol Methods* **91**, 106–113.
134. Tedersoo L, Tooming-Klunderud A, Anslan S (2018) PacBio metabarcoding of Fungi and other eukaryotes: errors, biases and perspectives. *New Phytol* **217**, 1370–1385.
135. Ritter CD, Dunthorn M, Anslan S, de Lima VX, Tedersoo L, Nilsson RH, Antonelli A (2020) Advancing biodiversity assessments with environmental DNA: long-read technologies help reveal the drivers of Amazonian fungal diversity. *Ecol Evol* **10**, 7509–7524.
136. Semenov MV (2021) Metabarcoding and metagenomics in soil ecology research: achievements, challenges, and prospects. *Biol Bull Rev* **11**, 40–53.
137. Sota T, Kagata H, Ando Y, Utsumi S, Osono T (2014) Metagenomic approach yields insights into fungal diversity and functioning. In: *Species Diversity and Community Structure*, Springer Briefs in Biology, Springer, Tokyo, pp 1–23.
138. Wu B, Hussain M, Zhang W, Stadler M, Liu X, Xiang M (2019) Current insights into fungal species diversity and perspective on naming the environmental DNA sequences of fungi. *Mycology* **10**, 127–140.
139. Ovaskainen O, Nokso-Koivisto J, Hottola J, Rajala T, Pennanen T, Ali-Kovero H, Miettinen O, Oinonen P, et al (2010) Identifying wood-inhabiting fungi with 454 sequencing – What is the probability that BLAST gives the correct species? *Fungal Ecol* **3**, 274–283.
140. Kubartová A, Ottosson E, Dahlberg A, Stenlid J (2012) Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Mol Ecol* **21**, 4514–4532.
141. Yamashita S, Masuya H, Abe S, Masaki T, Okabe K (2015) Relationship between the decomposition process of coarse woody debris and fungal community structure as detected by high-throughput sequencing in a deciduous broad-leaved forest in Japan. *PLoS One* **10**, e0131510.
142. Runnel K, Tamm H, Lõhmus A (2015) Surveying wood-inhabiting fungi: most molecularly detected polypore species form fruit-bodies within short distances. *Fungal Ecol* **18**, 93–99.
143. Vaz AB, Fonseca PL, Leite LR, Badotti F, Salim AC, Araujo FM, Cuadros-Orellana S, Duarte AA, et al (2017) Using next-generation sequencing (NGS) to uncover diversity of wood-decaying fungi in neotropical Atlantic forests. *Phytotaxa* **295**, 1–21.
144. Hyde KD, Baldrian P, Chen Y, Chethana KW, De Hoog S, Doilom M, De Farias AR, Gonçalves MF, et al (2024) Current trends, limitations and future research in the fungi? *Fungal Divers* **125**, 1–71.
145. Su W, Xu R, Bhunjun CS, Tian S, Dai Y, Li Y, Phukhamsakda C (2022) Diversity of *Ascomycota* in Jilin: introducing novel woody litter taxa in *Cucurbitariaceae*. *J Fungi* **8**, 905.
146. Afshari N, Gomes de Farias AR, Bhunjun CS, Phukhamsakda C, Hyde KD, Lumyong S (2023) *Distoseptispora dipterocarpi* sp. nov. (*Distoseptisporaceae*), a lignicolous fungus on decaying wood of *Dipterocarpus* in Thailand. *Curr Res Environ Appl Mycol* **13**, 68–78.
147. Afshari N, Karimi O, Gomes de Farias AR, Suwannarach N, Bhunjun CS, Zeng XY, Lumyong S (2023) Additions to *Diatrypaceae* (*Xylariales*): Novel taxa and new host associations. *J Fungi* **9**, 1151.
148. Hyde KD, Saleh A, Aumentado HD, Boekhout T, Bera I, Khyaju S, Bhunjun CS, Chethana KW, et al (2024) Fungal numbers: global needs for a realistic assessment. *Fungal Divers* **128**, 191–225.
149. Bajpai A, Johri BN (2019) Climate change is real: Fungal perspective. *Kavaka* **53**, 12–21.