

Chapter 8

History, challenges, and opportunities in the study of entomopathogenic fungi in tropical regions: Borneo as a model ecosystem

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Abstract

Fungal pathogens tend to have a poor reputation as a disease among the general public and policy-makers. However, entomopathogenic fungi, adapted to infect and kill arthropod hosts, play a wide range of roles in ecosystems, provide key ecosystem services, and offer interesting models to understand pathogen interaction networks. Tropical regions provide especially favorable conditions for studying this highly diverse group of fungi and their infection patterns across environmental and landscape disturbance gradients. In this chapter, we review the current state of knowledge on entomopathogenic fungi in tropical ecosystems, with a focus on the island of Borneo, which we present as a useful model system for their study. We briefly present how research on these fungi has evolved from early taxonomic work to more recent molecular and integrated approaches, and summarize what is currently known – and still poorly understood – about their diversity, ecological roles, the ecosystem services they provide, and the influence of biotic and abiotic factors. We also highlight some of the key challenges and opportunities associated with studying entomopathogenic fungi in the tropics. These regions are among the most biodiverse on the planet, but also among the most threatened. A better understanding of these poorly studied fungi will help clarify how their diversity is structured, how they interact with other organisms, and how they respond to environmental change, ultimately supporting their conservation and their integration into biocontrol and ecosystem management strategies.

Keywords: Species interaction, ecosystem management, biocontrol, knowledge shortfall, arthropod-associated fungi

1. Introduction

Fungi are generally understudied and commonly harbour cryptic diversity, with only 3-8% of existing species described (Hawksworth and Lücking, 2017). Many, particularly moulds and pathogenic species, also tend to have a poor reputation among members of the public due to their association with disease and decay (Singara Charya, 2015). However, their beneficial roles for medicine and food are more generally known. Recently, they have gained increasing recognition for their important roles in ecological systems, such as nutrient cycling (Aerts, 2003; Stark, 1972) and population control (Ben Fekih *et al.*, 2026; Vega and Blackwell, 2005). Fungi are omnipresent and interact with a myriad of organisms, including plants, animals and other fungi (Aerts, 2003; Santamaria *et al.*, 2023; Woodward and Boddy, 2008).

Arthropods and fungi commonly interact with one another through mycophagy or symbiosis (Santamaria *et al.*, 2023; Vega and Blackwell, 2005). Mutualistic associations benefit both the fungus and the arthropod (Rutkowski *et al.*, 2023). Other associations are commensal in which one benefits but the other remains unaffected. Parasitic associations benefit one party (parasite or pathogen) at the cost of the other party, which is negatively impacted (Araújo and Hughes, 2016; de Groot *et al.*, 2026). Pathogens can be the direct cause of host death, whilst parasites lower host fitness and only indirectly contribute to death (Kaishian *et al.*, 2024; Onstad *et al.*, 2006).

Entomopathogenic fungi (EPF) are pathogens adapted to infect and kill arthropod hosts across a wide range of taxa (Araújo and Hughes 2016). They can regulate host population densities and thus mediate natural and agricultural biocontrol (Kobmoo *et al.*, 2025; Kreutz *et al.*, 2004). Certain groups of EPF, such as the *Ophiocordyceps* genus, have the fascinating ability to manipulate the behaviour of their hosts (de Becker *et al.* 2021). Also known as "zombie fungi", they orchestrate host behavior in a way that maximizes the chances of their own reproductive success (Andersen *et al.*, 2009). The infected host body serves as a nutrient source for the fungi to develop and eventually produce new spores (Vega *et al.* 2012). *Ophiocordyceps* infecting ants can reach even 100% prevalence across colonies (Loreto *et al.*, 2014). These fungi belong to multiple taxonomic lineages, including Microsporidia, Chytridiomycota, Zygomycota, Basidiomycota, and Ascomycota (Araújo and Hughes, 2016). The Hypocreales order is the largest group of EPF, with a host range spanning 12 insect orders. It also includes some of the better-known EPF species, which are important pathogens, such as *Ophiocordyceps*, *Cordyceps*, *Hypocrella*, and *Moelleria* (Araújo and Hughes, 2016). In turn, EPF can also be infected by hyperparasitic fungi such as *Niveomyces* and *Torrubiellomyces* (Araújo *et al.*, 2022).

These remarkable fungi remain understudied, and they have received considerably less attention than fungal plant pathogens (Vega and Blackwell, 2005). With recently increased awareness of these fungi (Figure 1), taxonomical efforts are being made, resulting in the description of many new species yearly (Araújo *et al.*, 2018; Khonsanit *et al.*, 2024). In 1994, 50,000 species of EPF were estimated to exist, and only 750 were described (Rossman, 1996; Mueller and Schmit, 2007; Hawksworth *et al.*, 1995). By 2011, estimates of the total

global fungal species richness more than tripled, suggesting that the expected number of EPF species would also be higher (Evans *et al.*, 2011). In 2016, Araújo & Hughes reported more than 1,500 described species. It is predicted that there are ten EPF species per host arthropod species (Hawksworth, 2001). These numbers indicate the importance of EPF in ecosystems, although this significance remains poorly documented.

Entomopathogenic fungi are widely geographically distributed, from temperate to tropical zones. However, they tend to be more diverse and abundant in tropical regions. Although empirical evidence is lacking, EPF belonging to the order Entomophthorales (e.g. *Entomophthora*) are reported more frequently in temperate regions (Hajek, 1997), whereas members of the order Hypocreales (e.g. *Ophiocordyceps*) are predominantly documented in tropical and subtropical regions (Araújo and Hughes, 2016; Vega *et al.*, 2012). As one of the largest islands of Southeast Asia, Borneo has great natural value that is represented in the large areas of Old World rainforest (Small *et al.*, 2004). Many endemic species from multiple taxa occur in tropical forests (Davis *et al.*, 2019; Merckx *et al.*, 2015; Neo *et al.*, 2021). Regardless of the fact that we commonly find EPF in forests of Malaysian Borneo (unpublished data), there are few published works discussing the diversity and distribution of EPF in this region, apart from some sporadic records in literature.

2. Historical trends of the study of entomopathogenic fungi: from taxonomy to molecular biology and integrated approaches

Early views of insect–fungus associations were shaped by the “vegetable wasp” and “vegetable caterpillar” concept, in which species of *Ophiocordyceps* and *Cordyceps* were mistaken for plant-like growths emerging from insect hosts (Cooke, 1982; Waterhouse, 1932). Subsequent taxonomic work firmly established these organisms as fungi, supported by detailed morphological and developmental studies conducted by early mycologists (Figure 1). By the late nineteenth century to the 1970s, research on EPF was largely taxonomic in focus, with foundational contributions by Roland Thaxter, who worked extensively on North American Entomophthorales (Thaxter, 1888), Thomas Petch, who advanced EPF taxonomy in Europe (Petch, 1931), and Yosio Kobayasi, whose 1941 monograph on the genus *Cordyceps* represented a major milestone in the field (Kobayasi, 1941; Samson *et al.*, 1988). As taxonomic frameworks became established, research interest expanded toward the potential application of EPF as biological control agents against agricultural pests, a theme that dominated mid-twentieth-century studies. This body of research, mainly focused on taxonomy and ecology, was followed by a relative decline in activity during the 1960s, then a steady increase from the 1980s onward (Figure 1), often as applied research (Ben Fekih *et al.*, 2026; Boykin *et al.*, 1984).

Renewed interest in EPF research emerged in the 2000s with advances in molecular biology, driving a shift from purely morphology-based taxonomy toward phylogenetic analyses and integrative approaches that combine molecular, morphological, and ecological data (Figure 1). Phylogenetic research was conducted almost exclusively within this integrative framework. The introduction of the one-species–one-name principle marked a significant advance in fungal systematics by unifying multiple morphs (i.e., teleomorphs and

anamorphs) within single taxa (Hawksworth *et al.*, 2011; Wingfield *et al.*, 2012). In parallel, recent phylogenetic reclassifications at higher taxonomic levels have substantially improved understanding of EPF evolution and taxonomy (Araújo *et al.*, 2018; Evans and Samson, 1984; Hywel-Jones, 1995; Khonsanit *et al.*, 2024, 2021; Sung *et al.*, 2007), as well as host specificity, infection mechanisms and behavioural manipulation of the host (Araújo and Hughes, 2016; De Bekker *et al.*, 2021; Mora *et al.*, 2018). Despite this progress, EPF remain understudied, and significant knowledge gaps persist. Compared to the rest of the fungal kingdom, research on EPF remains less extensive, and research fields such as molecular phylogenetics and integrative approaches have emerged much later in their history (Figure 1).

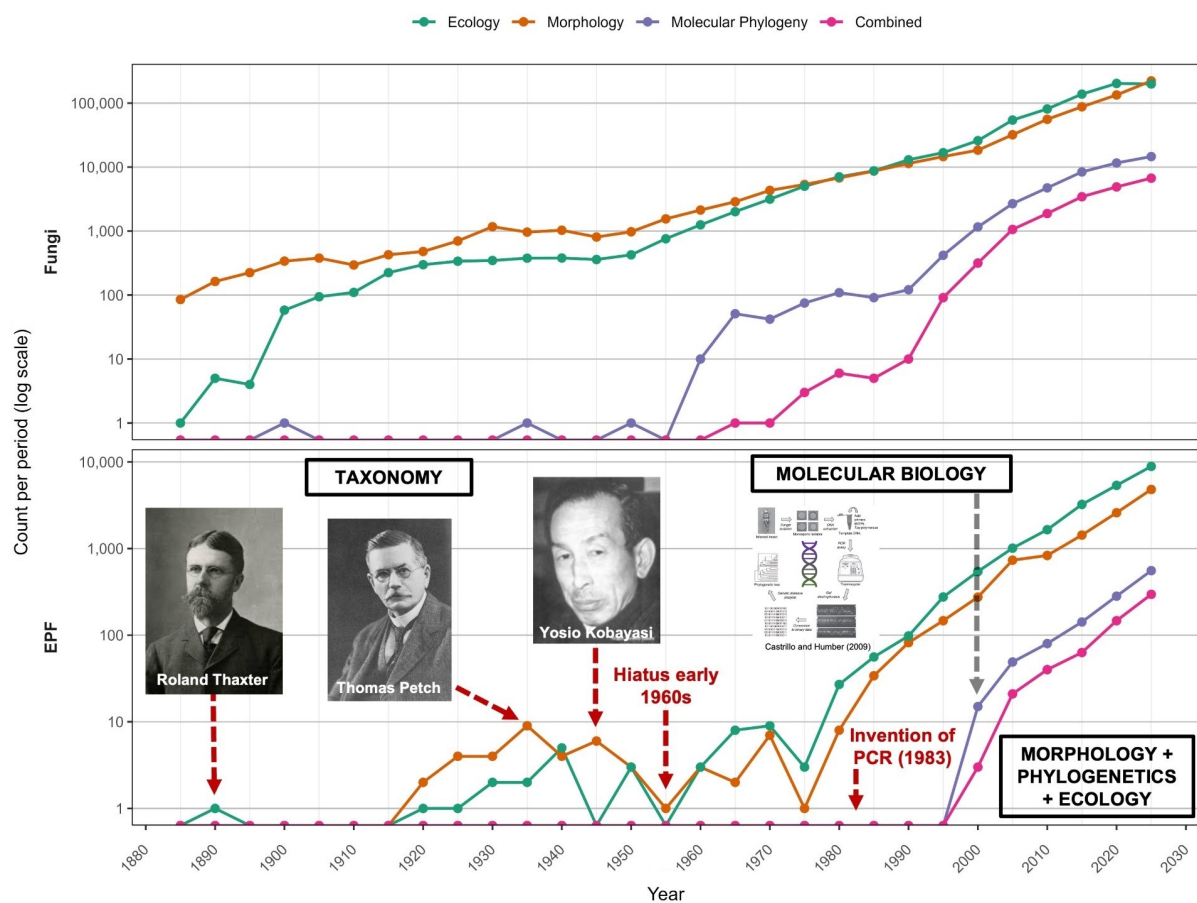


Figure 1. History of research output on entomopathogenic fungi (EPF) across disciplines (1880-2025). The number of publications since the previous year mark is shown at 5-year intervals. Data were generated using Google Scholar literature searches for “fungi” and “entomopathogenic fungi”, with the addition of the following keywords (including parentheses): “morphology”; “molecular phylogeny”; “ecology”; as well as their combination: “morphology” “molecular phylogeny” “ecology”. Searches were filtered to consider respective time intervals (e.g. the 1885 mark counts works published from 1st January 1880 to 31st December 1884) and excluded citations. Publication years were manually verified for searches returning up to 10 results, to account for incorrect listings that could affect the observed pattern, particularly in early periods with low record counts. Note that the molecular phylogeny trend for fungi is inflated by a journal name that matches the search query. Image by F.C.D.W., J.C. and M.L.

Currently, investigations in this group are driven by several key factors: (1) advances in molecular biology enabling the identification of novel species and the resolution of longstanding taxonomic ambiguities; (2) the development of ecological frameworks to examine host–pathogen interactions and habitat associations, with implications for conservation and biodiversity management; and (3) the growing demand for sustainable alternatives to chemical pesticides, as well as the bioprospecting of fungal metabolites with potential pharmaceutical value.

3. What we know and don't know

3.1 Species diversity of entomopathogenic fungi in the tropics

A reasonable number of studies have investigated EPF taxonomy in the Neotropics (notably Brazil, Colombia), and Southeastern Asia (notably China, Thailand), while the Afrotropics remain severely understudied (De Wint *et al.*, 2024). Novel and morphologically distinct forms of EPF continue to be discovered, while cryptic diversity has received increasing attention over the past two decades, largely due to advances in molecular techniques (Araújo *et al.*, 2018; Mongkolsamrit *et al.*, 2022). Despite Borneo being part of the biodiversity-rich Sundaland region, the species diversity of EPF in this area remains poorly documented. In the 19th and 20th centuries, a small numbers of sporadic observations were made in Malaysian Borneo (De Wint *et al.*, 2024): *Ophiocordyceps gentilis* (Cesati, 1879), *Ophiocordyceps humbertii* (Petch, 1935), *Ophiocordyceps oxycephala* (Petch, 1934). In 2019, *Ophiocordyceps dipterigena* was found in Brunei (De Wint *et al.*, 2024). Recently, elaborate inventories were made in Sabah (Malaysian Borneo), notably including regions of Mt. Kinabalu, Danum Valley and Maliau Basin Conservation Areas (DVCA, MBCA) (unpublished data), which will form the first baselines of EPF diversity and biogeography of Borneo. The first of these articles adds five species to this list, resulting in a preliminary total of nine species currently known for Borneo: *Cordyceps jakajanicola*, *Cordyceps tenuipes*, *Blackwellomyces calendulinus*, *Purpureocillium lilacinum*, and *Simplicillium formicae* (Shahbaz *et al.*, 2026a). The second article reports four more species isolated from spiders, but it remains unclear if these are entomopathogenic, hyperparasitic or saprophytic in nature: *Leptobacillium geminatum*, *L. leptobactrum*, *L. symbioticum*, *L. coffeanum* (Shahbaz *et al.*, 2026b). This study also reports the first two hyperparasites on entomopathogenic fungi from Borneo: *Simplicillium formicae* and *S. puwenense*.

Further systematic documentation of EPF species and their associated hosts in Borneo will facilitate the development of a comprehensive morphological and sequence-based reference database. This effort will also establish standardized field-sampling protocols, including essential equipment for specimen collection (Figure 2) and methodologies for processing highly sensitive material prior to downstream phylogenetic analyses in the laboratory (Figure 3). Resulting phylogenetic analyses will provide insights into the evolutionary relationships among EPF taxa and their hosts, contributing to a deeper understanding of their diversity, ecology, and evolutionary history.

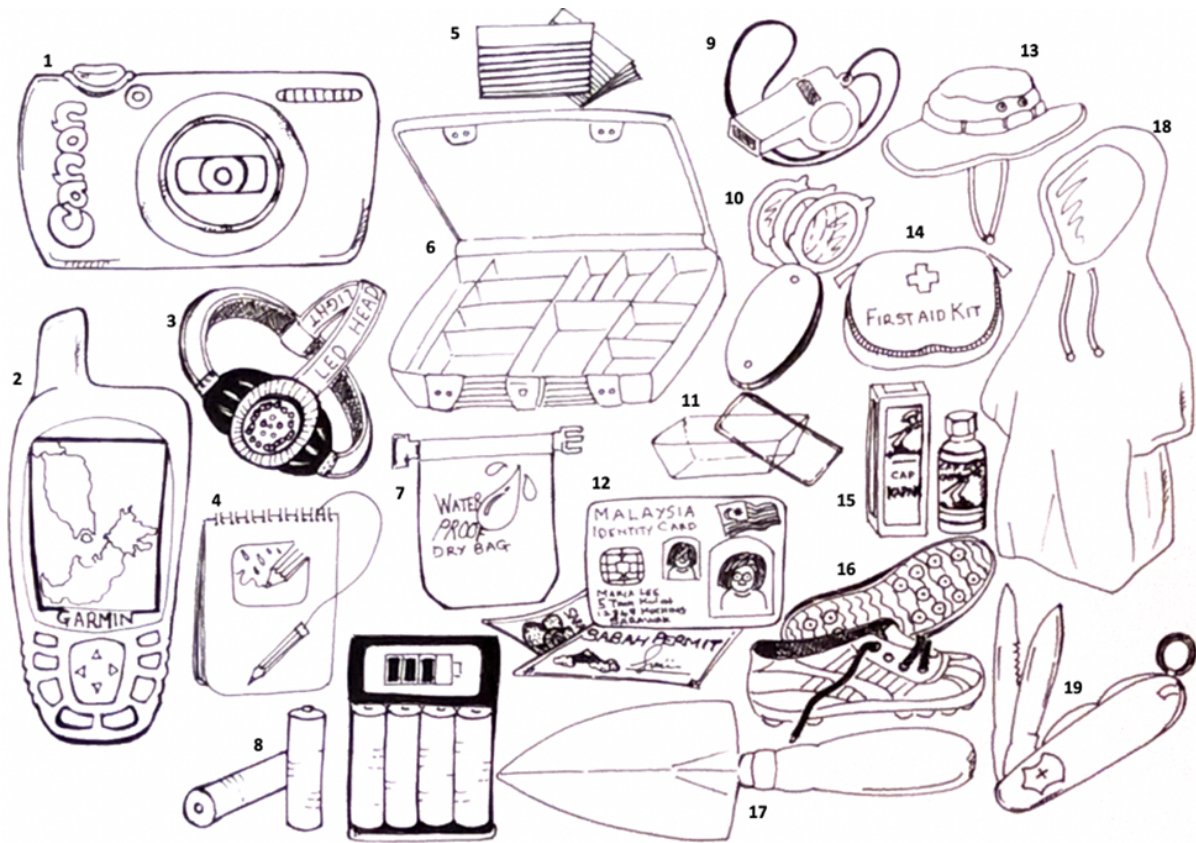


Figure 2. Essential field equipment for sampling entomopathogenic fungi in Borneo. 1. Camera to document specimens in the field; 2. GPS device to mark location of sampling; 3. Headlamp to access caves and navigate in the dark; 4. Waterproof field notebook and pencil; 5. Index card for notes to be placed next to the specimen in sampling container; 6. Fishing tackle box used as sampling container; 7. Waterproof dry bag to store electronic devices and personal documents; 8. Rechargeable batteries and charger; 9. Whistle to signal for distress call; 10. Hand lens; 11. Additional plastic container to collect samples; 12. Personal documents such as identification card and field access permits; 13. Jungle army hat; 14. First aid kit; 15. Oil containing a blend of eucalyptus, menthol, camphor, and other essential oils effective in removing leeches; 16. Inexpensive rubber shoes that are waterproof, easy to dry, and have good traction on varying terrain for hiking in tropical jungle; 17. Trowel to dig up samples buried deep in the ground; 18. Rain poncho to stay dry during the rainy season; and 19. Pocket knife. Image by M.L.

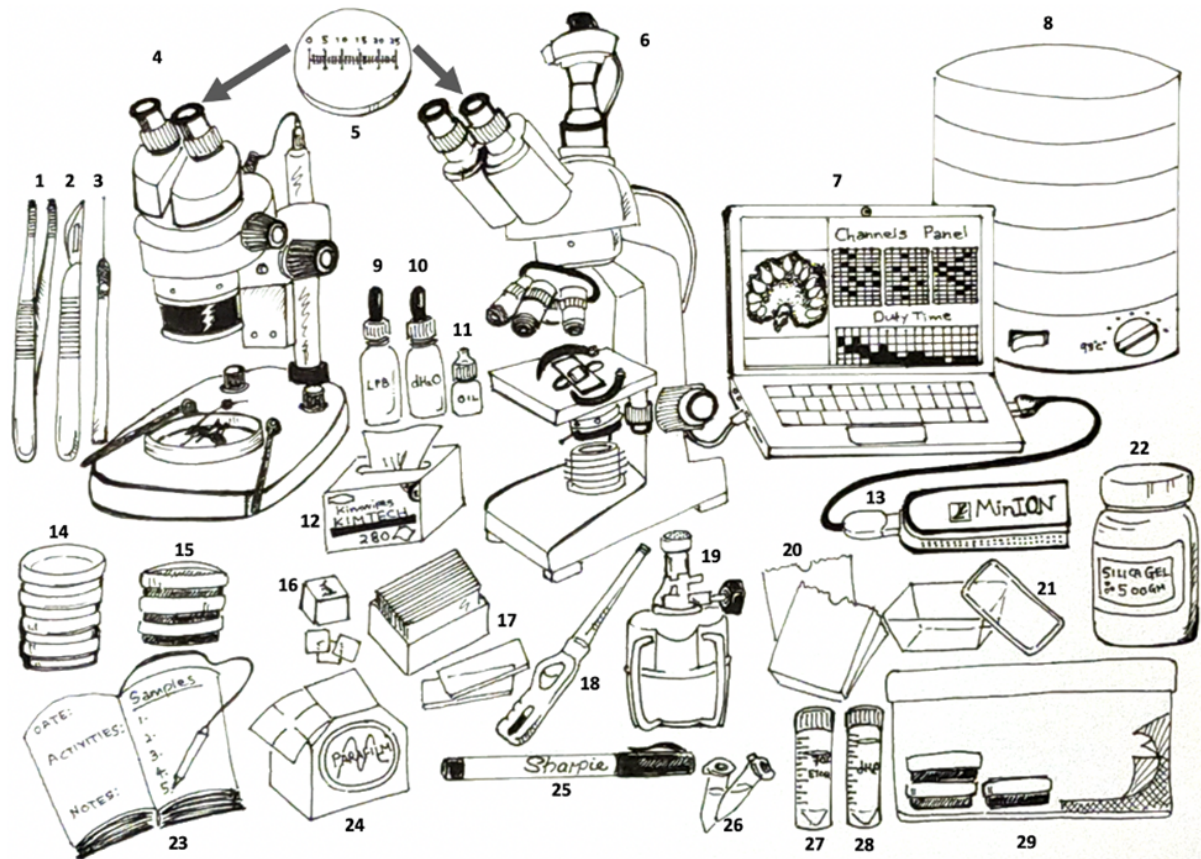


Figure 3. Specimen processing materials and equipment used for use in a field laboratory prior to specimen transport back to a research laboratory for down-stream work in phylogenetics. 1. Forceps; 2. Scalpel; 3. Inoculating needle; 4. Dissecting microscope; 5. Ocular micrometer for both the dissecting and light microscopes; 6. Light microscope with camera attached (Optional); 7. Laptop; 8. Food dehydrator to dry specimens for transport; 9. Lactophenol Cotton Blue to dye specimens for visualization under the light microscope; 10. Distilled water in dropper bottle to wet samples for visualization under the light microscope; 11. Immersion oil; 12. Lab wipes; 13. MinION making DNA sequencing possible in remote areas with limited resources; 14. Empty sterile Petri dishes; 15. PDA media plates to culture selected specimens in the field; 16. Cover slips; 17. Slides; 18. Gas lighter; 19. Portable Bunsen burner; 20. Wax paper to begin vouchering specimens with duplicates in order to distribute to local Forestry Department herbarium or Biodiversity Center for further collaborative research; 21. Additional plastic container to save samples for getting crushed during transport; 22. Silica gel to keep specimens dry; 23. Field notebook; 24. Parafilm; 25. Indelible marker pen; 26. 1.5ml microcentrifuge tubes containing 2X CTAB to store specimens for future molecular work; 27. Flat bottom 50ml centrifuge tube containing 70% ethanol as flaming alcohol; 28. Sterile distilled water in flat bottom 50ml centrifuge tube to moisten paper towel for the humidity chamber; and 29. Plastic tub with moist paper towel to serve as a humidity chamber. Image by M.L.

3.2 Ecological functions and ecosystem services provided by entomopathogenic fungi in the tropics

Interactions between species affect the stability of ecosystems and the diversity of ecological communities (Chesson, 2000; Jordán, 2009). Host-specific natural enemies can promote ecosystem stability and maintain diversity by ensuring no species can become highly dominant (Chesson, 2000; Jonsson *et al.*, 2017; Letourneau *et al.*, 2009). Entomopathogenic

fungi have been established as natural enemies of arthropods (Vega *et al.*, 2012), and their biocontrol properties have been investigated for regulating dominant arthropod populations in natural ecosystems (Kreutz *et al.*, 2004; Mann and Davis, 2021) as well as agricultural pests (Kobmoo *et al.*, 2025; McGuire and Northfield, 2020). Previous work has particularly focused on two globally distributed EPF with a wide insect host range, *Metarhizium* and *Beauveria* spp., which are the most commonly available EPF used in tropical agroecosystems for biological control applications (McGuire and Northfield, 2020). Such EPF can suppress major pest populations and improve plant growth in agricultural conditions (Kobmoo *et al.*, 2025). Some EPF in Borneo can act as antagonists against strains of *Ganoderma boninense* fungus, likely due to their metabolic and enzymatic arsenal capable of breaking down fungal cell walls, and may have promising applications for managing basal stem rot in oil palm plantations (Shahbaz *et al.*, 2026a). However, evidence from natural systems is scarce, and the extent to which these fungi regulate natural host populations, as well as their role in maintaining tropical biodiversity, is still not fully understood.

The impact of EPF on arthropods is likely mediated by conspecific negative density dependence, which has been proposed as an explanation for biodiversity maintenance across a wide range of taxa, from terrestrial to marine animals (Albery *et al.*, 2020; Connell *et al.*, 1971; Janzen, 1970). Natural enemies, such as pathogens, are expected to be limited by their ability to disperse between hosts. Higher host densities facilitate pathogen transmission among individuals, leading to higher infection rates (Albery *et al.*, 2020; Hochachka and Dhondt, 2000). Due to this negative density dependence, the resulting stronger pathogen pressure lowers the maximum host population size, i.e. the size where mortality is equal to population growth. Host negative density dependence might play an important role in arthropod population control and biodiversity maintenance by pathogens. In addition, pathogens impose evolutionary pressure on their hosts, forcing host species to evolve and adapt, maintaining genetic diversity in the process (Hamilton, 1982). Further research is needed to determine whether EPF mediate biodiversity maintenance through negative density dependence.

From an applied research perspective, these ecological functions are also potentially important. The development of pest management strategies based on locally occurring EPF could reduce reliance on synthetic pesticides by providing safer, environmentally sustainable alternatives. Systematic chemical profiling of EPF species will facilitate the identification and isolation of bioactive metabolites with potential insecticidal properties. In addition, fungal secondary metabolites may offer promising avenues for pharmaceutical research, including the discovery of compounds with potential anticancer and therapeutic applications. Ultimately, the capacity to uncover and utilize such natural products can inform conservation policies aimed at maintaining balanced and climate-resilient ecosystems, while also supporting sustainable economic opportunities for local communities in Borneo.

3.3 Influence of biotic and abiotic factors on entomopathogenic fungi and their hosts in Borneo

Like other fungi, EPF are influenced in many ways by their environment, with which they constantly interact. Entomopathogenic fungi are known to interact with other species in bitrophic or multitrophic interactions, most importantly with arthropods and plant hosts (Araújo and Hughes, 2016; Onstad *et al.*, 2006; Van Roosmalen and De Bekker, 2024). Many EPF show specificity towards arthropod hosts, but this specificity remains largely unknown for plant hosts (Andriolli *et al.*, 2025; Araújo *et al.*, 2018; Khonsanit *et al.*, 2024, 2021; Will *et al.*, 2023). The availability of hosts forms an important biotic condition that limits (Araújo and Hughes, 2016) or at least reduces (Shah *et al.*, 2023) the presence of EPF. Other organisms also compete with EPF, such as fungi, bacteria and nematodes (Sheng and St. Leger, 2024; Wang *et al.*, 2023; Wu *et al.*, 2018).

In their meta-analysis, Gielen *et al.* (2024) found that infection rates by EPF tend to be higher in the tropics, and that there are latitudinal differences in EPF community composition, with Hypocreales being more prevalent in tropical regions compared to Entomophthorales which are more prevalent in temperate regions. However, as the authors point out, the reasons behind these patterns are not clear, since they may partly reflect biases in the volume of research conducted in the tropics compared to more temperate regions. Still, they raise interesting questions and hypotheses to test to help better understand the potential biological and eco-evolutionary drivers behind these patterns. Many interactions involving EPF remain understudied, as do the nature and direction of these interactions and their potential implications for biocontrol. For example, EPF acting as plant endophytes, plant disease antagonists, rhizosphere colonizers, or plant growth promoters as highlighted by Vega *et al.* (2009). Biotic interactions involving EPF are often overlooked and understudied in natural settings, especially in the tropics and in complex environments such as soils (e.g., interactions between EPF and entomopathogenic nematodes in soil, Půža and Tarasco 2023, Wong and Wong 2025).

The occurrence, prevalence and persistence of EPF can be influenced by a variety of abiotic factors, including climate (e.g., temperature, humidity) and the environmental conditions of the habitats from which they are isolated (e.g., soil), which can, for example, affect spore survival and fungal growth (Qayyum *et al.* 2021; Jaronski 2009). Some EPF have temperature tolerances that allow them to grow under tropical climatic conditions, which are generally favorable for their growth, development and spread (Yazid *et al.* 2020). Species of EPF isolated from soil samples have also been shown to exhibit preferences for certain elevations on a temperate mountain in China (Feng *et al.*, 2025). Understanding how EPF species and their biotic interactions respond to environmental changes is important for knowing where these interactions occur, under which conditions, and how to better integrate them into biocontrol strategies and ecosystem management plans. For EPF in epigeal habitats, temperature appears to be a key factor controlling fungal virulence, while UV radiation is also an important factor affecting the activation and depletion of conidia for EPF in hypogeous habitats (Quesada-Moraga *et al.* 2024). McGuire and Northfield (2020) proposed testable hypotheses for *Metarhizium* suggesting that abiotic factors are the main

determinants of population genetic structure at higher latitudes, whereas biotic factors play a larger role at lower latitudes. In the tropics, particularly in Borneo, more research should be encouraged to investigate the effects of abiotic factors, in synergy with biotic factors, on EPF communities and infection prevalence, especially in comparison with regions that differ in climate and host communities. For example, Lavery *et al.* (2021) investigated the spatial dynamics of ants infected by *Ophiocordyceps unilateralis* s.l. in Gunung Mulu National Park, Sarawak, Borneo, and found that the height at which infected ants were located was likely linked to specific temperature and humidity conditions that favor spore dispersal and fungal growth. Further investigations should consider relationships between tropical EPF and key biotic and abiotic factors, including elevation, humidity, cumulative precipitation, habitat disturbance (e.g., primary forest, secondary forest, degraded land, or agricultural plantations), host abundance and developmental stage (larval, pupal, or adult), and host death location (e.g., leaf undersides, leaf litter, or decaying wood).

4. Challenges and opportunities of studying entomopathogenic fungi in the Borneo Challenges

The limited empirical literature on EPF in Borneo can be attributed to several challenges faced by researchers. Highly biodiverse ecosystems in the tropics typically involve complex ecological interactions, where species such as EPF and their arthropod hosts interact with a wide range of organisms, including other fungal species, plants and microorganisms (Barlow *et al.*, 2018). These complex webs of interdependencies can obscure the ecological dynamics, and hence make it challenging to identify and isolate specific ecological factors that affect EPF and their arthropod hosts (Haelewaters *et al.*, 2026; Hesketh *et al.*, 2010).

Furthermore, field sites in Borneo are often in remote areas where the terrain is harsh and inaccessible (Abdullah, 2017), making the transport of researchers and equipment difficult and expensive. The limited infrastructure and facilities, such as electricity and clean water, can exacerbate the situation by hindering on-site fungal sample processing (Sánchez Herrera *et al.*, 2024). Even when on-site sample processing is feasible, researchers encounter the potential degradation of EPF due to repeated fluctuations of abiotic conditions, such as temperature and humidity, during storage, transportation, or shipping (Quesada-Moraga *et al.*, 2024). Moreover, research in natural habitats (e.g. pristine forests) often requires lengthy permit and compliance documentation processes, complicating logistical planning for fieldwork in the tropics (Metcalf *et al.*, 2025). Nevertheless, appropriate permits should be obtained to ensure legal conduct of research, as some publications featuring Borneo collections have been (or might be) retracted due to permit issues (Freitag *et al.*, 2019, 2018).

Research indicates that about 61% (22 out of 36) of the world's biodiversity hotspots are located in tropical regions, primarily within developing countries across Africa, Asia, and South America (Hrdina and Romportl, 2017). These regions often face limited research funding and resources (Livingston *et al.*, 2016), with governmental priorities typically concentrated on sectors such as human health, societal welfare, technology advancement

and agricultural development (Confraria *et al.*, 2024), leaving little support for research on EPF taxonomy, natural history and ecological studies on EPF. The equipment needed for ecological and molecular studies is both specific and expensive, and it is unlikely to be obtained and maintained without sufficient financial support (Cazabonne *et al.*, 2022). This is likely to lead to a lack of training opportunities, which in turn results in a shortage of taxonomists specializing in EPF (Paknia *et al.*, 2015). Furthermore, approaches that distribute international funding and collaboration to a narrow and limited group of institutions and nations in the tropics can create disparities in EPF research opportunities (Metcalf *et al.*, 2025).

The differences in working culture between local and international collaborators can also present significant challenges in the research of EPF (Haelewaters *et al.*, 2021b). These cultural disparities include communication styles, expectations regarding collaboration, decision-making procedures, and research priorities, which can lead to misunderstanding and ultimately reduced overall research productivity in EPF. Besides, there is insufficient collaboration among mycologists, entomologists, and ecologists, which are the three main fields necessary for understanding EPF and their roles in tropical environments (Haelewaters *et al.*, 2021a).

Opportunities

The tropics offer numerous research opportunities in the field of EPF, with Borneo as an ideal example due to its high biodiversity. The Borneensis Herbaria at Universiti Malaysia Sabah (BOR) has established an EPF collection since 2015 (n = 2436; both specimens and cultures; personal communication). In addition, the *Checklist of Fungi of Malaysia* documents over 3,000 fungal species across various groups in Peninsular and Borneo Malaysia (Chua *et al.*, 2012). To facilitate further research on EPF, it would be worthwhile to collect and actively maintain EPF records from Borneo in a publicly accessible, centralized database, including key information such as taxonomy, geographical distribution, morphological characteristics, and host associations (e.g. De Wint *et al.* 2024).

As an island, Borneo also offers a unique chance to study EPF and their host associations from an eco-evolutionary dynamics and biogeography perspective (Stallman *et al.*, 2024). With its geographical isolation and rich biodiversity, Borneo can serve as a natural living laboratory to study how EPF and their host co-evolve and adapt in response to specific ecological pressures over time. Consequently, this allows us to understand the historical and contemporary biogeographical factors, such as climate, landscape alteration, and species migration and colonization, that may shape these relationships.

Studies on EPF can be performed at both spatial and temporal scales in Borneo. Various landscapes with different ecosystems on this island provide an opportunity to study how spatial heterogeneity influences EPF and their arthropod hosts across space and time. Considering the essential ecological roles of EPF and ongoing anthropogenic global change, the tropics, including Borneo, are among the most vulnerable regions (Pereira *et al.*, 2024). It

is therefore vital to identify the key drivers of anthropogenic disturbance that impact EPF and the consequences for the functions they support in both natural and semi-natural ecosystems. For instance, future work could fruitfully examine EPF communities along a gradient of landscape degradation (e.g. from pristine forest to monoculture forest) or assess the impact of non-native EPF invasion on native EPF and their arthropod hosts (St. Leger, 2021), as done for microparasitic fungi by Xie *et al.* (2026). These studies would provide valuable insight into the ecological dynamics of EPF communities, particularly through potential negative density dependence mechanisms (Gielen *et al.*, 2024).

We did not find any formal information as to whether EPF are commercially deployed in Borneo as biocontrol agents for pest management among local farmers and industries. This gap presents a possibility for collaboration between academic institutions and both the industrial and smallholder sectors in the research and development of EPF strains suitable for field application. Besides, Borneo also provides a significant opportunity for discovering new EPF strains with potential disease and pest control capabilities (Shahbaz *et al.*, 2026a). These opportunities extend beyond laboratory studies to include field-based applications, enabling a deeper understanding of the ecosystem services provided by EPF and contributing to a reduction in reliance on chemical pesticides in agricultural systems.

Beyond their implications for biocontrol and plant growth (Kobmoo *et al.*, 2025), these systems provide useful models for studying complex multitrophic interactions and for addressing evolutionary questions related to host specificity, pathogenicity and genome evolution, particularly in host-specialist EPF that occur almost exclusively in tropical ecosystems, as is the case in the genus *Metarhizium* (Bidochka and Small, 2005). Integrating ecological surveys with taxonomic and phylogenetic studies of EPF in Borneo will enable robust statistical analyses and the development of ecological models to explain patterns of population distribution and species interactions. These data will further disclose host–pathogen interactions and help us understand EPF dynamics within their natural environments. Interdisciplinary collaboration, particularly between trained entomologists and mycologists, is critical for accurate identification of both invertebrate hosts and their associated fungal pathogens.

Finally, studying EPF in the tropics can be greatly enhanced through the potential of citizen science by engaging a broad range of participants, including local communities, scientists such as mycologists, and personnel from both governmental and private sectors (Haelewaters *et al.*, 2024). This collaborative approach enhances data observation (e.g. via photographs) and collection, particularly in remote areas, contributing to the discovery of new EPF species and associations without placing a significant financial burden on projects (e.g. Irga *et al.* 2020, Crous *et al.* 2021). Moreover, citizen science helps build research networks and foster partnerships between local communities, universities, and various agencies, bridging gaps between scientific research and local knowledge (Haelewaters *et al.*, 2026, 2024). This collaboration can result not only in raising awareness about the ecological role of EPF, but also in leading to more holistic approaches to conservation and resource management.

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