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CHARACTERIZATION OF THE MYCOBIOME OF *RAFFLESIA* SEEDS: THEIR POTENTIAL ECOLOGICAL ROLES AND APPLICATIONS IN *RAFFLESIA* PROPAGATION AND CONSERVATION

BY

FERUZA KARNITSKIY

A MASTER'S THESIS SUBMITTED TO THE FACULTY OF COLLEGE OF SCIENCE, LONG ISLAND UNIVERSITY

IN PARTIAL FULFILLMENT OF REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

MAY 2023

MAJOR
BIOLOGY

DEPARTMENT
LIFE SCIENCES

CERTIFIED BY:

Dr. Joseph Morin
Chairman of the Department

Date May 11, 2023

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Dr. Timothy Leslie

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ABSTRACT

The plant microbiome exerts a profound influence on plant health, growth, and life cycle. This ecosystem comprises diverse microbial communities, such as symbiotic endophytes, mycorrhizal fungi, epiphytes, saprophytes, rhizobia, and pathogens, which inhabit parasitic and non-parasitic plants. *Rafflesia speciosa*, a holoparasitic plant, is a unique and endangered species that depends on its host *Tetrastigma* spp. for survival. In this study, fungal metagenomics was conducted to characterize the fungal community—the mycobiome within *Rafflesia* seeds, and a phylogeny was reconstructed. The ecophysiological characteristics of these fungal genera were also researched in the literature, and their primary ecological trait, whether plant mutualist, saprotroph, phytopathogen, mycoparasite, or entomopathogen, was mapped on the phylogeny to explore phylogenetic patterns. The majority of the identified fungal genera were Ascomycete fungi. There was no phylogenetic pattern detected in the ecophysiological traits of *Rafflesia* seed fungi, suggesting that these traits have evolved repeatedly throughout the fungal phylogeny as ecological adaptations. Characterization of *Rafflesia*'s seed mycobiome allowed us to gain insights on the potential ecology of these fungi and possible roles and applications in the ex situ propagation and conservation of *Rafflesia* species.

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INTRODUCTION

Rafflesia produces the largest single flowers in the world, up to a meter in diameter. It is a holoparasitic plant that lacks roots, stems, and leaves, obligately dependent on its sole host vine, *Tetrastigma.* There are about 40+ known species of *Rafflesia* unique to the fast disappearing forests of Southeast Asia (Govaerts *et al.,* 2021). Hidayati and Walck (2015) suggested that increase in diversity among *Rafflesia* species could be attributed to favorable conditions in the rainforest during the Mid-Miocene to Pliocene period. The Rafflesiaceae family to which *Rafflesia* belong also includes other holoparasites such as *Sapria* and *Rhizanthes,* which are all parasitic to *Tetrastigma* (Nais, 2001). *Rafflesia* and *Sapria* are the only known plants to date that have lost their chloroplast genome (Molina *et al*. 2014; Cai *et al*. 2021) and have no photosynthetic abilities, though plastid compartments were detected at least in *R. philippensis.* It is suspected that *Rafflesia* retains these plastids for non-photosynthetic metabolic finctions such as synthesis of lipids and amino acids (Ng *et al*., 2018). Molina *et al*. (2023) discovered how *Rafflesia* seeds become transcriptionally active after imbibition and prepare for germination upon host stimulation. As per transcriptome results, *Rafflesia* lack plastome and high prevalence of transposable elements, some of which were horizontally transferred from the host (Molina *et al.,* 2023). Additionally, as a nonphotosynthetic holoparasite, *Rafflesia* seeds share "core parasitism genes" found in Orobanchaceae (Molina *et* al., 2023) and there is evidence that *Rafflesia* may acquire its host's genes, expressing them for its own benefit (Xi *et al.,* 2012).

Hidayati and Walck (2015) mentioned that *Rafflesia*'s flowering occurs seasonally, during the hottest and driest time of the year, with *R. kerri* having open flowers from January to March. The estimated length of the life cycle of *Rafflesia* is 3-4.5 years. *Rafflesia* flower buds can take years to emerge from its host *Tetrastigma*, with 90% of the buds dying before flowering, and it takes 9-16 months for the buds to develop before flowering (Molina *et al*., 2017). Anthesis can last up to 7 days depending on the species. *Rafflesia* is primarily unisexual, with mostly male individuals (Molina *et al*., 2017). The flower attracts carrion flies and other pollinators by emitting a scent that mimics rotting flesh, which aids in its pollination process (Molina *et al*., 2017). After pollination, the plant produces fruits that take six to eight months to mature, yielding over 200,000 seeds (Molina *et al*., 2017). The small seeds of *Rafflesia* have multiple potential dispersal agents, including wild pigs, ground squirrels, ants, termites, pangolin, and elephants, but small mammals are probably the most effective agents for seed dispersal (Hidayati and Walck, 2015). Ants are also possible seed dispersers (Pelser *et al.* 2016). However, it is unknown how the seed germinates in the host (Wicaksono *et al*., 2020).

Hidayati and Walck (2015) highlights the main threat to *Rafflesia* populations as habitat loss due to logging, collection of firewood, and conversion of forests to housing or monoculture plantations such as rubber, palm oil, and fruit gardens. Thus, Molina *et al*. (2017) have been working to conserve *Rafflesia* due to the urgent concerns of climate change and the destruction of tropical forests. The exotic requirements of *Rafflesia* make it difficult to propagate in the United States, and scientists still have much to learn about its seed dispersal, germination, and other ecological needs (Molina *et al*., 2017). Molina *et al*. (2017) have tried to propagate *Rafflesia* species from the Philippines in an American botanical garden using horticultural techniques such as rooting and grafting *Rafflesia*-infected cuttings, and inoculation of *Rafflesia* seed in the host, but have yet to succeed. Molina *et al.* (2017) think that *Rafflesia* may rely on microbial symbionts to grow inside the host.

Indeed, plants in any ecosystem interact with both beneficial and harmful organisms, creating a complex web of spatial and temporal associations (De Vega *et al.,* 2010). Recent research has emphasized the significance of connecting multiple interactions, including those between above- and belowground biota, to understand ecological and evolutionary processes in nature (De Vega *et al.,* 2010). Mycorrhizae are a group of fungi that exist in a mutualistic relationship with plants, crops, and trees, and help improve the health and fertility of the soil they grow in (Giovannini *et al*., 2020). Their use in agriculture and horticulture as natural fertilizers and pesticides is becoming increasingly popular in order to sustain the production of healthy foods on a global scale (Giovannini *et al.,* 2020). Mycorrhizal fungi can enhance plant growth and health by improving nutrient uptake, fixing nitrogen, solubilizing phosphorus, producing phytohormones, siderophores, and releasing antibiotics into the soil (Giovannini *et al*., 2020). Additionally, there are fungal endophytes, which are microorganisms that live within plant tissues and promote plant growth from within (Porras-Alfaro and Bayman, 2011). These endophytes can be beneficial or pathogenic, and can inhabit plant tissues such as stems, shoots, and leaves, changing from beneficial to pathogenic throughout the plant's life cycle (Porras-Alfaro and Bayman, 2011).

Fungal endophytes, as well as bacterial endophytes, have crucial beneficial roles in the development and physiology of their host plants, including improved stress tolerance, enhanced root growth, and provision of special nutrition and water (Cui, Vijayakumar, and Zhang, 2018). It is believed that through extended periods of co-evolution, endophytes establish unique relationships with each other and can significantly impact the formation and accumulation of specific key metabolic products, thus affecting the quality and quantity of crude drugs derived from medicinal plants (Cui, Vijayakumar, and Zhang, 2018). Unfortunately, limited knowledge exists regarding the factors influencing host-endophytic relationships and endophyte assembly in plant-parasitic interactions (Cui, Vijayakumar, and Zhang, 2018). There are different types of fungal endophytes and they can be classified as either plant mutualists, saprotrophs, phytopathogens, mycoparasites, and/or entomopathogens. A plant fungal mutualist provides benefits to its plant host (Diaz-González *et al*., 2020); a saprotroph, derives nutrition from decaying matter (Promputtha *et al.,* 2007); a phytopathogen causes harm and disease to the plant host (Peng *et al.,* 2021); a mycoparasite, parasitizes other fungi (Jeffries, 1995); and an entomopathogen, kills or disables insects (Vega *et al*., 2008).

Some parasitic plants are found more frequently on plants associated with mycorrhizae, indirectly benefiting the parasite through increased biomass and flower production (De Vega *et al*., 2010). However, in some cases, arbuscular mycorrhizal fungi of the host plant can reduce the germination, attachment, and emergence of the parasite, thereby reducing damage to the host. Therefore, endophytic holoparasitic plants, such as those in the Rafflesiaceae family, provide a good opportunity to establish a tripartite association between the parasitic plant, mycorrhizal fungus, and host plant (De Vega *et al*., 2010).

The objective of this study was to characterize the fungal endophytic community within *Rafflesia* seeds and determine their ecophysiological traits (whether plant mutualist, saprotroph, entomopathogen, mycoparasite, phytopathogen, or unknown) to gain insights on their potential ecological roles and applications in the ex situ propagation of *Rafflesia* species.

MATERIALS AND METHODS

Two seed samples of *Rafflesia speciosa* were surface-sterilized with 2% sodium hypochlorite, rinsed and sent for ITS ZymoBIOMICS targeted sequencing (cat# Q2003) to Zymo Research, Irvine CA. Raw sequence files were loaded in OmicsBox (Biobam Bioinformatics, Valencia, Spain) and assembled using default settings for “Megahit Metagenomic Assembly”. The resulting contigs were blasted against the NCBI nr/nt reference database with “Entrez query Fungi[orgn]” with “maximum hit=1” e-val<1 e-100 in Geneious Prime (Biomatters Ltd, Auckland, New Zealand). Sequence reads were taxonomically classified based on top blast hit and phylogenetically analyzed using PhyML as implemented in Geneious prime. Abundance data from Zymo for fungal taxa was mapped on the phylogeny. Comperehensive literature review of ecophysiological characteristics of the fungal genera was conducted and categorized whether plant mutualist, saprotroph, phytopathogen, mycoparasite, and/or entomopathogen, with these “traits” mapped on the phylogeny using ITol http://itol2.embl.de/

RESULTS

The analysis revealed 83 fungal genera between the two *Rafflesia* seeds. Using information from scientific literature, the ecological notes on the various fungal genera present in *Rafflesia* seeds were summarized (Table 1). In addition, the primary ecophysiological traits - saprotroph, phytopathogen, mycoparasite, plant mutualist, entomopathogen, or other/unknown – were characterized. Multiple categories were allowed per fungal genus if there was such evidence in the literature. Among the 83 genera found, nine were classified as entomopathogenic fungi, two were identified as plant mutualist fungi, five were categorized as mycoparasitic fungi, 27 were classified as phytopathogenic fungi, 34 were identified as saprotrophic fungi, and 31 were unknown. In addition to their ecophysiological characteristics, the fungal genera represented a total of 50 families and 29 orders. 69 percent (57/83) of the fungal genera belonged to the phylum Ascomycota and the order Hypocreales. Unfortunately, 43.6% of the endophytic fungi in the two *Rafflesia* seeds sampled could not be classified, meaning they are not represented in the database and may represent new taxa.

Table 1. Fungal genera identified within *Rafflesia* seeds and their ecological roles from the literature.

Phyla	Order	Family	Genera	Ecological information	Ecophysiological characteristic
Ascomycota	Hypocreales	Hypocreaceae	Acremonium	Gliotoxin produced by *Acremonium* can inhibit Pythium (Anisha and Radhakrishnan, 2017).	Entomopathogen
Ascomycota	Pleosporales	Didymosphaeriaceae	Alloconiothyrium	*Alloconiothyrium* are widespread saprobes (Tennakoon *et al*., 2022).	Saprotroph
Ascomycota	Onygenales	Onygenaceae	Amauroascus	Polyphyletic *Amauroascus* are dimorphic fungi that can cause mycosis in mammals. Can be found in carnivore dung, in	Saprotroph

				agricultural soil, and growth is restricted to environmental sources (Kandemir *et al.,* 2022).	
Ascomycota	Orbiliales	Orbiliaceae	Arthrobotrys	*Arthrobotrys* are nematophagus fungi that are abundant in rhizosphere soils (Rodrigues *et al*., 2009).	Entomopathogen
Ascomycota	Eurotiales	Aspergillaceae	Aspergillus sp.	*Aspergillus* species can be opportunistic pathogens causing infections after drought, insect damage, or other environmental stresses. Also, majority are saprobic decomposers (Pennerman *et al*., 2020).	Saprotroph, Phytopathogen, Other/Unknown
Ascomycota	Dothideales	Dipodascaceae	Aureobasidium	*Aureobasidium puppulans* infects organic remnants and decaying vegetable plants (Riedl, 1972).	Phytopathogen
Ascomycota	Xylariales	Xylariaceae	Biscogniauxia	*Biscogniauxia* are opportunistic pathogens found on old and stressed trees causing infections like charcoal canker and grapevine trunk disease due to phytotoxins (Bahmani *et al*., 2021).	Saprotroph, Phytopathogen.
Ascomycota	Hypocreales	Nectriaceae	Campylocarpon	*Campylocarpon fasciculare* is a soil-borne fungi that causes black-foot disease in root and stem bases of grapevines by colonizing dead and dying plant material (Abeywickrama *et al*., 2021).	Saprotroph
Ascomycota	Saccharomycetales	Unidentified	Candida	*Candida* is the most heterogenous taxa of yeasts and has antifungal, novel, and reversible adaptive resisistances (Akins, 2005; Suzuki and Nakase, 1998).	Saprotroph, Other/Unknown
Ascomycota	Glomerellales	Plectosphaerellaceae	Chordomyces	*Chordomyces* are saprobes (Wijayawardene *et al*., 2017).	Saprotroph, Other/Unknown
Ascomycota	Capnodiales	Cladosporiaceae	Cladosporium	Cladosporiaceae cause vegetable plant decay and can spread on organic remnants (Riedl, 1972).	Phytopathogen
Ascomycota	Saccharomycetales	Metschnikowiaceae	Clavispora	*Clavispora lusitaniae* 146 showed mycoparasitism against *Penicillium digitatum* in postharvest fungal disease in lemons (Pereyra *et al*., 2020).	Saprotroph, Mycoparasite, Other/Unknown
Ascomycota	Hypocreales	Bionectriaceae	Clonostachys	*Clonostachys* have multi-trophic lifestyles including saprobes in soil and dead organic	Saprotroph, Mycoparasite, Mutualist, Other/Unknown

				matter, mutualists in rhizospheres, and necrotrophic mycoparasites by killing and feeding on their mycohosts (Piombo *et al*., 2023).	
Ascomycota	Chaetosphaeriales	Chaetosphaeriaceae	Codinaeopsis	Ascomycete fungi and a Class 2 endophyte (Morgan-Jones, 1978; Rodriguez *et al*., 2009).	Other/Unknown
Ascomycota	Glomerellales	Gloeophyllaceae	Colletotrichum sp.	*Colletotrichum tofieldiae* strain Ct0861 mutualist to *Arabidopsis thaliana,* maize (*Zea mays* L.) and tomato (*Solanum lycopersicum*) (Diaz-Gonzalez *et al*., 2020). Pathogenic *Colletotrichum* species are hemibiotrophic where the initial infection is asymptomatic followed by necrotrophic phase (Kleeman *et al.,* 2012).	Mutualist, Phytopathogen
Ascomycota	Diaporthales	Schizoparmeaceae	Coniella	*Coniella* are widespread plant pathogens common as parasites causing fruit, foliar, leaf, stem, and root diseases (Alvarez, Groenewald & Crous, 2016).	Phytopathogen
Ascomycota	Hypocreales	Nectriaceae	Cosmospora	*Cosmospora* are considered fungicolous fungi which a diverse group of organisms associated with other fungi which can be found on bark or stromatic pyrenomycetes (Rossman, Farr & Akulov, 2008).	Mycoparasite
Basidiomycota	Tremellales	Cryptococcaceae	Cryptococcus sp.	*Creptococcus* are known as the most heterogenous taxa of yeasts (Suzuki and Nakase, 1998). Saprotrophic *C. podzolicus* and *C. terricola* are found on the surface of roots and in therhizosphere (Buee *et al*., 2009); Mycoparasitic *Cryptococcus luteolus* is effective against *Alternaria porri* (Ellis) Ciferri (Tyage, Dube and Charaya, 1990); Some species are pathogenic as well (Dupont *et al*, 2016).	Saprotroph, Mycoparasite, Phytopathogen, Other/Unknown
Ascomycota	Saccharomycetales	Phaffomycetaceae	Cyberlindnera	Phytopathogenic *C. amylophila* was spread in diseased pine wood trees (Liu *et al*., 2021); *Cyberlindnera* was found in Dendroctonus-bark beetles where females	Saprotroph, Mycoparasite, Phytopathogen, Other/Unknown

				can harbor microbes in organs called mycetangia (Vazquez-Ortiz *et al*., 2022).	
Ascomycota	Hypocreales	Nectriaceae	Cylindrocladiella	*Cylindrocladiella* spp. are soil-borne fungi and as pathogens can cause diseases in crop plants such as leaf spots, root, stem, and cutting rots (Lombard *et al*, 2012).	Phytopathogen
Ascomycota	Diaporthales	Valsaceae	Cytospora	*Cytospora* has bioactivity to produce anti-fungal and anti-bacterial metabolites to restrict the growth of *Candida albicans* (Refaei *et al*, 2011).	Saprotroph, Mycoparasite
Ascomycota	Saccharomycetales	Debaryomycetaceae	Debaryomyces	*Debaryomyces* are found in soils, waters, plants, foods, and clinical specimens growing rapidly at pH 3.0-8.0 (Praphailong & Fleet, 1999).	Phytopathogen
Ascomycota	Chaetothyriales	Herpotrichiellaceae	Exophiala	Ascomycete fungi and a Class 2 endophyte (Carmichael, 1966; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Glomerellales	Plectosphaerellaceae	Furcasterigmium	Ascomycete fungi and a Class 2 endophyte (Giraldo & Crous, 2019; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Nectriaceae	Fusarium	Low abundance of *Fusarium* in soil and asymptomatically colonizes coastal beaches (Rodrigues *et al*., 2009). *F. oxysporum* is able to produce its' host metabolites such as podophyllotoxin, taxol, ginkgolide B, vincristine, and vinblastine (Anisha and Radhakrishnan, 2017).	Entomopathogen
Basidiomycota	Polyporales	Ganodermataceae	Ganoderma	*Ganoderma* is a pathogenic decomposer in mycorrhizia group (Parlucha *et al*., 2021). It causes white rot disease in various tree species resulting in the break down of structural components of wood by simultaneous decay and selective delignification (Loyd *et al*., 2018).	Phytopathogen
Basidiomycota	Geastrales	Geastraceae	Geastrum	*Geastrum* are gasteroid fungi which are found in in Quezon Protected Landscape (QPL) (Parlucha *et al.,* 2021) in China and in Wunvfeng National Forest Park in Northeast China (Tuo *et al*., 2022).	Saprotroph, Mutualist, Other/Unknown
Ascomycota	Saccharomycetales	Dipodascaceae	Geotrichum	*Geotrichum* spp. are ubiquitous saprotrophic	Saprotroph, Phytopathogen

				fungi (Antoniassi *et al.,* 2013). *Geotrichum candidum* is a filamentous hemiascomycete fungus which causes sour rot disease of fleshy fruits and citrus (Gold, Casale, & Keen, 1991).	
Ascomycota	Hypocreales	Nectriaceae	Gliocephalotrichum	*Gliocephalotrichum* species can cause postharvest diseases and fruit rot of tropical plants while causing lesions, soaked exocarp, mesocarp, and endocarp, and mycelium reaching deep into the seed (Silva *et al.,* 2020).	Phytopathogen
Ascomycota	Hypocreales	Nectriaceae	Gliocladiopsis	*Gliocladiopsis* is a plant pathogen which has bioactivity against *Pythium myriotylum* (a soil-borne oomycete necrotroph) (Anisha and Radhakrishnan, 2017).	Phytopathogen
Ascomycota	Hypocreales	Bionectriaceae	Gliomastix	*Gliomastix murorum var. felina* is a saprotroph (Kwa´sna *et al*., 2021).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Nectriaceae	Glionectria sp.	*Glionectria tenuis* found in soil samples in China (Lombard & Crous, 2012).	Saprotroph
Basidiomycota	Gloeophyllales	Gloeophyllaceae	Gloeophyllum	Wood-degrading *Gloeophyllum* sp. are basidiomycetes and are know as brown rot fungus (Presley *et al*., 2020).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Saccharomycodaceae	Hanseniaspora	Budding yeast, Ascomycete fungi *H. uvarum* is found on mature fruits and grapes as part of the fermentation microbiome. It also has mycoparasitic qualities against fungi that are responsible for mold development on fruits (Hanseniaspora, 2020; (Albertin *et al*., 2016).	Phytopathogen, Mycoparasite
Ascomycota	Pleosporales	Didymosphaeriaceae	Kalmusia	Ascomycete fungi and a Class 2 endophyte. *Kalmusia variispora* is associated with grapevine trunk disease in Iran (Hongsanan *et al*., 2020; Rodriguez *et al.*, 2009; Abed-Ashtiani *et al*., 2019).	Phytopathogen
Ascomycota	Saccharomycetales	Incertae	Kodamaea	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Kodamaea, n.d.; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Debaryomycetaceae	Kurtzmaniella	*Kurtzmaniella* are budding yeast, Ascomycete fungi, and a	Phytopathogen

				Class 2 endophyte associated with rotting wood, mushroom and tree bark samples collected in Brazilian ecosystems and in French Guiana. (Lachance & Starmer, 2008; Rodriguez *et al*., 2009; Lopes *et al*., 2019).	
Ascomycota	Botryosphaeriales	Botryosphaeriaceae	Lasiodiplodia	*Lasiodiplodia* species are Ascomycetes and Dothideomycetes with some of the species being ubiquitous and pluvivorous. Most species are plant pathogens causing leaf lesions, fruit and root rot, dieback, and cancers (Douanla-Meli and Scharnhorst, 2021). *L. theobromae* was found in crawling insects, primarily ants and danaid butterfly, *Idea leuconoe* (Nago and Matsumoto, 2014).	Phytopathogen, Entomopathogen
Ascomycota	Hypocreales	Cordycipitaceae	Lecanicillium	*Lecanicillium* spp. are mitosporic fungi known as entomopathogens. They are pathogenic against insects, phytoparasitic nematodes or fungi. Some species are mycoparasites though colonization of host plant tissues and resulting in disease resistance (Goettel *et al*., 2008).	Entomopathogen, Mycoparasite
Ascomycota	Saccharomycetales	Saccharomycetaceae	Limtongozyma	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Boontham *et al.,* 2019; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Lipomycetaceae	Lipomyces	*Lipomyces* are budding yeast, Ascomycete fungi, and a Class 2 endophytes that are from beach forest soils and they have the ability to grow in the absence of external nitrogen sources and utilize heterocyclic compounds (Kurtzman & Smith, 2011; Rodriguez *et al*., 2009; Yurkov, Kemler, & Begerow, 2011).	Phytopathogen
Ascomycota	Hypocreales	Nectriaceae	Mariannaea	*Mariannaea* are saprotrophic fungi and *M. humicola* is the first marine saprotrophic strain (Purahong *et al*., 2019).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Pichiaceae	Martiniozyma	Budding yeast, Ascomycete fungi, and a Class 2 endophyte	Saprotroph, Other/Unknown

				(Kurtzman, 2015; Rodriguez *et al*., 2009).	
Ascomycota	Chaetothyriales	Herpotrichiellaceae	Minimelanolocus	Ascomycete fungi and a Class 2 endophyte (Castaneda Ruiz & Heredia, 2000; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Mucoromycota	Mucorales	Mucoraceae	Mucor	Mucoralean fungi are mostly saprotrophs common od decaying plant matter using available simple carbohydrate molecules (Pawlowska *et al.,* 2019; Botha & du Preez, 1999). Also, plant pathogens *M. piriformis* causes post-harvest decay of fruits, and *M. indicus* and *M. circinelloides* are able to produce mycotoxins (Botha & du Preez, 1999).	Saprotroph, Phytopathogen
Ascomycota	Glomerellales	Plectosphaerellaceae	Musicillium	*Musicillium* are Ascomycete fungi and a Class 2 endophytes which cause cigar-end rot of bananas (Zare *et al*., 2007; Rodriguez *et al*., 2009).	Phytopathogen
Ascomycota	Saccharomycetales	Lipomycetaceae	Myxozyma	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Kurtzman & Smith, 2011; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Pichiaceae	Nakazawaea	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Kurtzman, 2011 (2); Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Nectriaceae	Nectria	*Nectria cinnabarina* is a plant pathogen and Hypocreales fungi which is found on hardwood trees and woody shrubs in temperate regions of the Northern Hemisphere. It's causes "coral spot" disease on apple and other hardwood trees (Hirooka, Rossman, & Chaverri, 2011).	Phytopathogen
Ascomycota	Amphisphaeriales	Sporocadaceae	Neopestalotiopsis	Phytopathogenic *Neopestalotiopsis* are Ascomycete fungi and a Class 2 endophytes in tropical and subtropical regions. They can cause leaf spot, dry flower, fruit rot, fruit scab, and trunk diseases. *N. drenthii* causes necrotic flower blight of *Macadamia integrifolia* (macadamia tree) in Australia	Phytopathogen

				(Maharachchikumbura *et al*., 2014; Rodriguez *et al*., 2009; Prasannath *et al*, 2021).	
Ascomycota	Saccharomycetales	Pichiaceae	Ogataea	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Yamada *et al*., 1994; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Thyridariaceae	Pleosporomycetidae	Parathyridaria	Ascomycete fungi and a Class 2 endophyte (Jaklitsch & Voglmayr, 2016; Rodriguez *et al.,* 2009).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Cordycipitaceae	Parengyodontium	Environmental saprobe *Parengyodontium album* was found in marine sediments and in indoor mineral materials (Belfiori, Rubini, & Riccioni, 2021). *C. vestitus* is a fungal mycelium that causes pistachio dieback (Hadj *et al.,* 2019).	Saprotroph, Phytopathogen, Other/Unknown
Ascomycota	Eurotiales	Aspergillaceae	Penicillium	Saprotrophic *Penicillium* lives on plant parts, soil, decaying organic substances, and plant residues. But some species are plant pathogens via production of mycotoxins and conidia/phialospores (Moretti and Sarroco, 2016; Riedl, 1972).	Saprotroph, Phytopathogen
Ascomycota	Togniniaceae	Togniniaceae	Phaeoacremonium	Plant pathogen *Phaeoacremonium* can infect with wide range of woody plants such as *Fraxinus latifola* by causing brown wood staining (Held *et al.,* 2021).	Phytopathogen
Basidiomycota	Polyporales	Meruliaceae	Phlebia	*Phlebia* are saprobes found in boreal and temperate forests as white rot type of decay on deciduous tree stumps, dead trunks and branches (Kuuskeri *et al*., 2016).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Pichiaceae	Pichia	*Pichia* can produce killer toxins that are lethal to other sensitive yeasts and filamentous fungi such as *Aspergillus, Candida,* and *Fusarium*. *Pichia* is also pathotroph-saprotroph-symbiotroph and an opportunistic pathogen (Sajid *et al.,* 2022; Azpiazu-Muniozguren *et al., 2021*).	Mycoparasite, Phytopathogen
Ascomycota	Pleurotheciales	Pleurotheciaceae	Pleurotheciella	*Pleurotheciella* are saprobes that are Ascomycete fungi and a Class 2 endophyte	Saprotroph, Other/Unknown

				(Reblova *et al*., 2016; Rodriguez *et al*., 2009; Lance *et al.,* 2020).	
Ascomycota	Hypocreales	Clavicipitaceae	Pochonia	*P. chlamydosporia* is a fungal egg parasite of root-knot and cyst nematodes found in barley, tomato, potato, or Arabidopsis (Ghahremani *et al*., 2019).	Entomopathogen.
Ascomycota	Pleosporale	Sporormiaceae	Preussia	Ascomycete fungi and a saprotroph (Lozano *et al.,* 2021).	Saprotroph
Ascomycota	Hypocreales	Nectriaceae	Pseudocosmospora	Phytopathogenic *Pseudocosmospora rogersonii* causes wood decay on *Verdeal-Transmontana* olive tree resulting in leaf damage (Markakis *et al*, 2017). Also, *Pseudocosmospora* species are hardly identified because of their decayed condition (Zeng & Zhuang, 2021).	Phytopathogen
Basidiomycota	Agaricales	Hymenogastraceae	Psilocybe	*Psilocybe* are a diverse genera of fungi and are found in the neotropic ecozone and in Mexico (De Mattos-Shipley *et al*., 2016).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Ophiocordycipitaceae	Purpureocillium	Entomopathogenic *Purpureocillium lilacinum* is a fungal endophyte that infects insect herbivores like cotton aphids and pathogenic insects. *P. lilacinum* is used as a biocontrol agent against root-knot nematode (Castillo Lopez *et al*., 2014).	Entomopathogen
Ascomycota	Pleosporales	Cucurbitariaceae	Pyrenochaeta	*Pyrenochaeta lycopersici* is a soil-living filamentous Ascomycete fungi and a Class 2 endophyte which causes Corky Root Rot (CRR) in tomato plants (Pyrenochaeta, n.d.; Rodriguez *et al*., 2009; Valente, Infantino, & Aragona, 2011).	Phytopathogen
Ascomycota	Chaetothyriales	Herpotrichiellaceae	Rhinocladiella	Ascomycete fungi and a Class 2 endophyte (Rhinocladiella, n.d.; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Basidiomycota	Sporidiobolales	Sporidiobola	Rhodosporidiobolus	*Rhodosporidiobolus* are marine fungi and can be found in the coastal waters of Southern China (Pham *et al.,* 2021).	Saprotroph, Other/Unknown
Ascomycota	Pleosporales	Thyridariaceae	Roussoella	Ascomycete fungi and a Class 2 endophyte (Roussoella, n.d.; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown

Ascomycota	Saccharomycetales	Saccharomycodaceae	Saccharomycopsis	Necrotrophic mycoparasite *Saccharomycopsis schoenii* can predate, attack, and kill variety of yeasts including *Candida auris* (Junker *et al*., 2019).	Mycoparasite
Basidiomycota	Tremellales	Trichomonascaceae	Saitozyma	Saprotrophic fungi *Saitozyma* can produce lipase to degrade fats (Li *et al*., 2022).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Dipodascaceae	Sporopachydermia	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Sporopachydermia, n.d.; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Incertae	Starmera	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Yamada *et al*., 1997; Rodriguez *et al*., 2009).	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Incertae	Starmerella	*Starmerella* are a budding yeast, Ascomycete fungi, and a Class 2 endophyte which are found in pollen and honey of stingless bees *Melipona quadrifasciata* and *Tetragonisca angustula.* The yeast also partakes in pollen and honey fermentation (Rosa & Lachance, 1998; Rodriguez *et al*., 2009; Santos *et al*., 2023).	Entomopathogen
Ascomycota	Eurotiales	Trichocomaceae	Talaromyces	*Talaromyces* are penicillum-like fungi found on dung due to their ability to grow at 37°C (Guevera-Suarez *et al*., 2019).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Tilachlidiaceae	Tilachlidium	*Tilachlidium* sp. (CANU-T988) was found on decaying wood in Christchurch, New Zealand (Feng *et al*., 2004).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Hypocreacea	Trichoderma	*Trichoderma* are saprobes found in forest soil, plant roots, and leaves (Oh *et al.,* 2018). As a common rhizosphere inhabitants, they can parasitize other fungi and compete with deleterious plant microorganisms (Contreras *et al*., 2016).	Saprotroph, Mycoparasite
Ascomycota	Chaetothyriales	Herpotrichiellaceae	Veronaea	Ascomycete fungi and dematiaceous mold which is abundant in healthy soil (Soto *et al*., 2017; Xu *et al*., 2012).	Saprotroph, Other/Unknown
Ascomycota	Hypocreales	Nectriaceae	Volutella	An opportunistic pathogen *Volutella buxi* causes volutella blight on ornamental boxwood	Phytopathogen

				resulting while infecting the plant's foliage, shoots and branches (Nbrazee, 2020).	
Basidiomycota	Wallemiales	Wallemiaceae	Wallemia	*Wallemia* are xerotolerant, xerophilic, and also halophilic species spread worldwide in saline and extreme environments (Azpiazu-Muniozguren *et al*., 2021).	Saprotroph, Other/Unknown
Ascomycota	Microascales	Microascaceae	Wardomycopsis	Ascomycete fungi and a Class 2 endophyte (Wardomycopsis, n.d.; Rodriguez *et al*., 2009)	Saprotroph, Other/Unknown
Ascomycota	Saccharomycetales	Phaffomycetaceae	Wickerhamomyces	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Kutzman *et al*., 2008; Rodriguez *et al*., 2009) *W. anomalus* survive in the insect (mosquito) gut and different mutualistic yeast-insect symbioses. It also acts as an antimicrobial agent (Cappelli, Favia, & Ricci, 2021).	Entomopathogen
Ascomycota	Hypocreales	Nectriaceae	Xenoacremonium	Saprotrophic *X. recifei* was found in non-phosphorous-amended soil and rhizosphere soil (Lombard *et al.,* 2015; Purahong *et al*., 2019).	Saprotroph, Other/Unknown
Basidiomycota	Hymenochaetales	Schizoporaceae	Xylodon	*Xylodon* are white-rot fungi which can grow on angiosperms and gymnosperms. They can be found on brown-rotten spruce stumps, palms or palm tree inflorescences, bamboo, ferns, and on the herbaceous *Staehelina dubia* L. and *Fallopia sachalinensis* (Cho *et al*., 2021).	Phytopathogen
Ascomycota	Saccharomycetales	Trichomonascaceae	Zygoascus	Budding yeast, Ascomycete fungi, and a Class 2 endophyte (Kurtzman and Robnett, 2007; Rodriguez *et al*., 2009)	Saprotroph, Other/Unknown

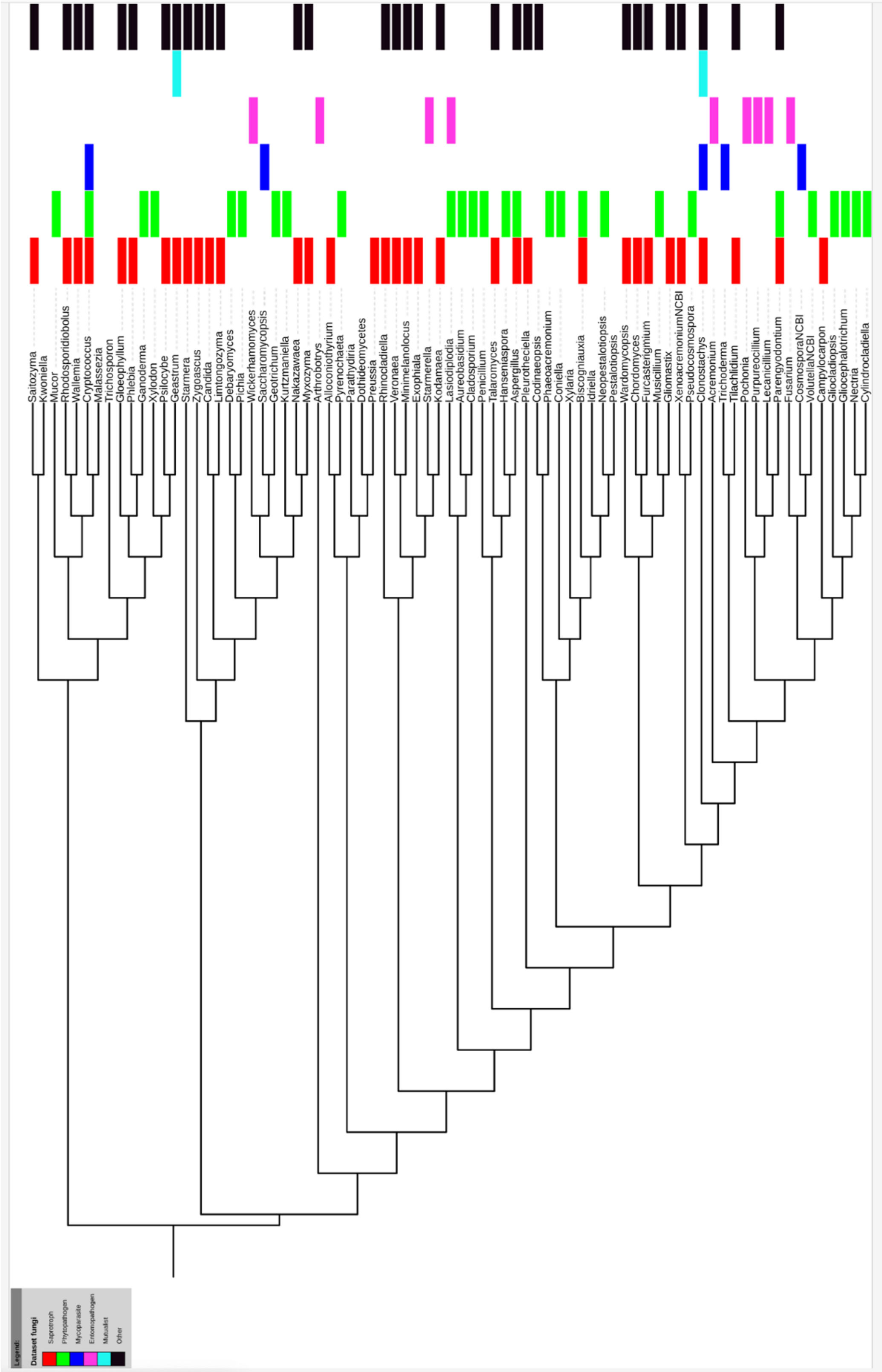

Figure 1. Phylogeny of the endophytic fungi in the *Rafflesia* seed mycobiome. The ecophysiological roles of these taxa according to the literature were mapped on the phylogeny.

DISCUSSION

The *Rafflesia* seed harbored a diverse mycobiome, with fungal genera belonging to Ascomycota and Basidiomycota phyla, which represents only 2 out of the 12 fungal phyla known so far (James *et al*., 2020). Based on literature, *Rafflesia* seed fungal endophytes were classified as either saprotrophs, phytopathogens, mycoparasites, plant mutualists, entomopathogens, and some unknowns (Table 1; Fig. 1). There was no phylogenetic pattern detected in the ecophysiological traits of *Rafflesia* seed fungi, such that the traits are scattered and not associated within a particular fungal clade, suggesting that these traits have evolved repeatedly throughout the fungal phylogeny as ecological adaptations (Fig. 1).

Phylum Ascomycota was the most diverse group within *Rafflesia*-associated fungi. Many species within Ascomycota are classified as Class 2 endophytes which have diverse ecophysiological properties (Rodriguez *et al*., 2009). Rodriguez *et al.* (2009) described them as the colonizers of various plant organs such as roots, stems, and leaves. They are also capable of forming extensive infections within plants and can spread through seed and/or rhizomes with high infection rates in plants growing in high-stress habitats (Rodriguez *et al*., 2009). Certain Class 2 endophyte fungal species are plant mutualists, having the ability to increase plant biomass, root and shoot growth, and provide tolerance against various biotic and abiotic stresses such as disease, drought, desiccation, heat, and salinity making them potential bio control agents and biofertilizers (Rodriguez *et al*., 2009). However, abundance of Class 2 endophytes is generally low in the rhizosphere, but some can inhabit agricultural fields without causing any apparent symptoms and colonize the roots, stems, and leaves of plants like watermelon (*Citrullus lanatus*) without inducing host defense systems (Rodriguez *et al*., 2009).

Another major fungal phylum represented within *Rafflesia* seed samples was phylum Basidiomycota. The difference between Basidiomycota and Ascomycota phylum is that Basidiomycetous fungi have longer mating periods (James *et al*., 2020), club shaped "fleshy" fruiting body (Jacinto, n.d.), and are more common in plant foliage than in soil (Rodriguez *et al*., 2009). While Ascomycete fungi are known as sac fungi due to their tube forming appereances (Unknown, n.d.).

This study on *Rafflesia* seed mycobiome helped us characterize its seed-associated fungal diversity and gain insights on their ecological traits, whether they are saprotrophs, entomopathogens, phytopathogens, and mycoparasites, and their potential role in *Rafflesia*'s life cycle. For example, saprotrophs are fungi with cosmopolitan distribution which obtain nutrients from dead or decaying organic matter (Tennakoon *et al*., 2022). The *Rafflesia* seed Ascomycete endophytes, *Veronaea* and *Trichoderma,* are saprophytes most commonly found in plant-associated environments such as forest soil, roots, and leaves (Xu *et al*., 2012; Oh *et al*., 2018). By breaking down decomposing matter, they recycle nutrients that conceivably benefits *Tetrastigma*, though their presence in *Rafflesia* seed is curious. It has been hypothesized that some fungal endophytes may be latent saprotrophs that switch to this new ecological role upon host senescence (Promputtha *et al.,* 2007). There were also Basiodiomycete endophytes in the *Rafflesia* seed such as *Gloeophyllum* and *Saitozyma* that not only serve as saprotrophs and promote nutrient cycling but also produce secondary metabolites (Presley *et al*., 2020; Li *et al*., 2022) that benefit their plant hosts, and conceivably could do the same for *Rafflesia* and/or *Tetrastigma*.

The mutualistic fungal endophyte *Colletotrichum* was also detected within *Rafflesia* samples. *Colletotrichum tofieldiae* strain Ct0861 has a mutualistic relationship with *Arabidopsis* *thaliana,* promoting plant growth and silique production under low phosphate conditions (Diaz-Gonzalez *et al.,* 2020). It was also found by Diaz-Gonzales *et al.* (2020) to promote growth in vitro of maize and tomato seedlings. Fungal endophytes colonize internal plant tissues without causing disease symptoms and establish mutualistic interactions with host plants, promoting growth and tolerance to stresses (Diaz-Gonzalez *et al*., 2020). Mutualist fungi such as *Colletotrichum* could provide beneficial conditions to both *Rafflesia* and its host plant *Tetrastigma*.

Of the classified seed fungal endophytes in *Rafflesia,* 69 percent (57/83) belonged to the Ascomycete order Hypocreales. Most entomopathogenic fungi described within *Rafflesia* species were within this order. Upon maturity, the *Rafflesia* fruit dehisces, revealing a coconut-scented white pulp holding the millions of *Rafflesia* seeds (Molina *et al.,* 2017). This is very attractive to various insects (beetles, flies, etc.) that feed on the pulp and/or lay eggs in it. Furthermore, ants such as *Technomyrmex* sp. and *Pheidologeton* sp. have been found inside the fruit wall of *Rafflesia philippensis* (Hidayati and Walck, 2015), drawn to the elaiosomes on the *Rafflesia* seed. The ants then carry the seeds back to their nest where they sprout and infect the root of nearby *Tetrastigma*, in effect facilitating *Rafflesia* seed dispersal. This diversity of insects associated with the *Rafflesia* fruit could explain why entomopathogenic fungi, which parasitize on insects, were detected as fungal endophytes.

There were also several fungal endophytes within the *Rafflesia* seed that were classified as phytopathogenic and presumably destructive to *Rafflesia*. Phytopathogens, to infiltrate plant host tissue, produce cell-wall degrading enzymes like pectinase, cellulase, and proteases (Peng *et al., 2021*) which are also enzymes produced by parasitic plants of *Orobanchaceae* (Yang *et al.,* 2015). It is possible that by harboring phytopathogenic fungi in its seeds, *Rafflesia* takes advantage of their cell-wall degrading enzymes to infect its own host *Tetrastigma*. Further studies are needed to confirm this.

This study on *Rafflesia* seed mycobiome helped us characterize its seed-associated fungal diversity and gain insights on their ecological traits, whether they are mutualists, saprotrophs, entomopathogens, phytopathogens, and mycoparasites, and their potential role in *Rafflesia*'s life cycle. Majority of the identified fungal genera were Ascomycete fungi. There was no phylogenetic pattern detected in the ecophysiological traits of *Rafflesia* seed fungi, suggesting that these traits have evolved repeatedly throughout the fungal phylogeny as ecological adaptations. Targeted studies could be conducted to better understand the role of specific fungal species in the life cycle of *Rafflesia*. Furthermore, collaborations between researchers in different fields such as plant biology, microbiology, and ecology could help generate new insights and promote a more holistic understanding of *Rafflesia* and its associated fungi. These studies could provide valuable information for conservation efforts aimed at protecting these unique and rare plants.

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