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Fungal endophytes: Insight into evolution, classification, and ecological functions in plants

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ABSTRACT

Fungal endophytes, symbiotic microorganisms inhabiting plant tissues, have attracted considerable interest due to their evolutionary, taxonomic, and ecological importance. This review seeks to elucidate fungal endophytes by examining their evolutionary origins, classification, and varied ecological functions within plant systems. The evolutionary path of fungal endophytes is analyzed, emphasizing their adaptive strategies and co-evolutionary interactions with host plants. The classification of these fungi is examined, highlighting the difficulties presented by their elusive lifestyles and the progress in molecular techniques that have enhanced their taxonomic identification. The review examines the ecological functions of fungal endophytes, specifically their contributions to plant stress tolerance, growth promotion, and interactions with other organisms. This review synthesizes current research, highlighting the significance of fungal endophytes in influencing plant health and ecosystem dynamics. This review aims to synthesize current knowledge, pinpoint deficiencies in understanding, and offer perspectives on future research avenues, thereby enhancing the application of fungal endophytes in agriculture, conservation, and biotechnology. This study emphasizes the complex relationship between fungal endophytes and their plant hosts, providing a comprehensive view of their evolutionary and ecological importance.

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Introduction

Fungal endophytes, microorganisms that inhabit plant tissues without causing disease, are integral to plant ecosystems. These symbionts contribute to plant health, stress resilience, and nutrient acquisition, playing a pivotal role in the colonization and diversification of land plants. They are recognized for their roles in helping plants withstand abiotic stresses such as drought, salinity, and extreme temperatures, as well as biotic stresses like pathogens and herbivores (Rodriguez et al. 2009). Endophytes contribute to plant fitness by producing secondary metabolites, including alkaloids, terpenoids, and flavonoids, which enhance plant defenses and attract beneficial organisms.

This diverse group of microorganisms are integral to plant survival and ecological success. They form complex and often mutualistic relationships with their host plants, influencing growth, stress tolerance, nutrient acquisition, and defense mechanisms. These interactions have co-evolved over hundreds of millions of years, beginning in the Paleozoic era when plants first colonized terrestrial environments. Their evolutionary history dates back to the Silurian and Devonian periods (approximately 400–500

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million years ago), when early plants partnered with fungi to overcome the challenges of terrestrial environments (Smith & Read 2008).

The transition from aquatic to terrestrial ecosystems posed numerous challenges for early plants, including desiccation, limited nutrient availability, and fluctuating environmental conditions. Fungi played a pivotal role in this transition, forming partnerships that enhanced nutrient uptake, particularly phosphorus and nitrogen, through associations such as those seen in arbuscular mycorrhizal fungi (AMF) (Smith & Read 2008). Fossil evidence from the Rhynie Chert, dating back over 400 million years, shows AMF colonizing the roots of some of the earliest land plants, highlighting the evolutionary significance of these symbiotic relationships (Taylor et al. 2006).

Over time, fungal endophytes diversified alongside their plant hosts, adapting to varying environmental conditions and forming intricate relationships that extend beyond nutrient exchange. The study of fungal endophytes offers valuable insights into plant adaptation and ecosystem dynamics. Their interactions with plants provide a unique perspective on co-evolution, as endophytes adapt to their host’s genetic and physiological traits while plants evolve mechanisms to regulate fungal colonization. This dynamic interplay has enabled plants to colonize diverse habitats, from arid deserts to tropical rainforests, underscoring the ecological and evolutionary importance of these symbiotic partnerships.

In modern times, the role of fungal endophytes extends beyond natural ecosystems. Advances in molecular biology and biotechnology have revealed their potential applications in pharmaceutics, medicine, agriculture, forestry, and environmental conservation (Abdel-Azeem et al. 2021; Motlagh et al. 2023; Abo Nouh & Abdel-Azeem 2024; Abo Nouh et al. 2024; Khader et al. 2024; Razaghi & Abdel-Azeem 2024 a, b; Mohamed & Abdel-Azeem 2024; Abdel-Azeem et al. 2024; Ibrahim & Abdel-Azeem 2025). Endophytes can be harnessed to develop stress-tolerant crops, reduce reliance on chemical fertilizers and pesticides, and restore degraded ecosystems (Hardoim et al. 2015).

This review delves into the continuous interaction between fungal endophytes and land plant evolution, exploring their origins, co-evolutionary dynamics, functional roles, and the factors influencing their distribution. By understanding these relationships, we can better appreciate the evolutionary journey of plants and the potential of fungal endophytes to address global challenges such as food security, climate change, and biodiversity conservation.

1- Evolutionary plant-fungal endophyte interaction

Fungal-plant symbiosis began during the colonization of terrestrial environments, with fossil evidence from the Rhynie Chert showing AMF in the roots of early land plants (Taylor et al. 2006). These fungi facilitated nutrient uptake, particularly phosphorus and nitrogen, in nutrient-poor soils, enabling early plants to thrive.

Bryophytes and other non-vascular plants likely relied on AMF to mitigate desiccation stress and enhance nutrient availability (Field et al. 2015). The mutualistic exchange of nutrients for carbon provided a foundation for vascular plant evolution and diversification, allowing plants to adapt to various terrestrial habitats.

The symbiotic relationship between fungi and plants is one of the oldest and most significant partnerships in the history of life on Earth. This relationship traces back over 400–500 million years to the Silurian and Devonian periods, when plants began transitioning from aquatic to terrestrial ecosystems. Fossil evidence from the Rhynie Chert, a 407-million-year-old sedimentary deposit, has provided compelling insights into these early interactions. These fossils revealed AMF colonizing the roots of early vascular plants, such as *Aglaophyton major*, highlighting the foundational role of fungi in enabling plant colonization of land (Taylor et al. 2006). Furthermore, these Fossil records show a crucial role in land life evolution (Niazi 2024).

The transition to terrestrial environments (terrestrialization) in fungi, characterized by the loss of the flagellum and the emergence of hyphal growth, represents a key evolutionary adaptation. Hyphal growth has likely evolved to enhance surface expansion in a saprotrophic lifestyle or to facilitate infection of larger organisms. As part of an evolutionary strategy that required penetrating living structures for nutrients, hyphal tips developed the ability to express numerous membrane transporters and secrete digestive enzymes. In this context, fungi's ability to regulate calcium metabolism independently of the extracellular environment may have been an adaptation for intracellular invasion, where free Ca^{2+} levels are insufficient as a reliable source. Similar specialized calcium homeostasis mechanisms have been observed in unrelated intracellular parasites such as Leishmania, Toxoplasma, and Plasmodium (Liu et al. 2015).

A number of different evolutionary scenarios could explain the colonization of land by fungi, which led to their enormous diversification. Improving our understanding of the microbial makeup of early soils and more accurate dating of significant occurrences like the spread of terrestrial fungus and the diversification of land plants are necessary to answer this topic. Because of their distinct emphasis on plants, soils, and ice, we call these alternative theories the "green," "brown," and "white" scenarios for the terrestrialization of fungus.

Fungal endophytes associations' exhibit varying degrees of specificity namely host specific relationships and generalist associations. Regarding the host-Specific Relationships, there are some fungi, like Epichloë species in grasses, have co-evolved with their hosts to produce specific defensive alkaloids (Saikkonen et al. 2010). For the generalist associations, many endophytes colonize multiple plant species, adapting to diverse environmental conditions and host traits (Arnold & Lutzoni 2007).

1.1. *Early Challenges and the Role of Fungi*

The shift from aquatic to terrestrial habitats posed several challenges for early plants like the desiccation where plants faced the risk of water loss in arid terrestrial environments, additionally the nutrient Acquisition (nutrients namely phosphorus and nitrogen were less accessible in early terrestrial soils. Additionally, the structural Support: plants required adaptations for vertical growth in the absence of buoyancy provided by water. Finally, the reproductive limitations: spores and gametes needed protection and mechanisms for dispersal in air.

Fungi were instrumental in addressing many of these challenges. AMF formed symbiotic relationships with the roots of early plants, creating networks that enhanced nutrient uptake, particularly phosphorus, in exchange for carbon from photosynthesis. This mutualism allowed plants to thrive in nutrient-poor soils and supported the development of more complex root systems (Field et al. 2015).

1.2. Co-evolution of Fungal Endophytes and Plants interaction

The co-evolution of plants and fungal endophytes is characterized by mutual adaptations. The endophytes evolved mechanisms to colonize plant tissues stealthily, avoiding host immune responses. These include the secretion of effector proteins and modulation of host gene expression (Hardoim et al. 2015). In the other hand, the host plants developed specialized structures like arbuscules and vesicles to facilitate fungal colonization and nutrient exchange. Plants also evolved chemical pathways to regulate symbiosis, such as the production of flavonoids and strigolactones (Gutjahr & Parniske 2013).

Fungal endophytes have significantly influenced plant evolution through their contributions to nutrient acquisition, defense mechanisms, abiotic stress tolerance and biochemical innovations. Indeed, AMF and dark septate endophytes (DSE) enhance the uptake of phosphorus, nitrogen, and trace elements, critical for plant survival in nutrient-deficient soils (Nutrient Acquisition) (Smith and Read, 2008). Besides, endophytes contribute to defense mechanisms by producing bioactive compounds that deter herbivores and pathogens, providing plants with an evolutionary advantage (Arnold & Herre 2003).

Furthermore, endophytes enhance tolerance to drought, salinity, and extreme temperature by producing osmoprotectants and modulating plant stress response pathways (Rodriguez et al. 2009). Finally, these symbiotic interactions have driven the evolution of plant secondary metabolites, such as alkaloids and terpenoids, which play roles in defense and ecological interactions (Pimentel et al. 2011). Therefore, these endophytic fungi contributions have allowed plants to colonize diverse ecosystems, from arid deserts to tropical rainforests.

1.3. *Factors influencing endophytic diversity*

This mutualistic relationship diversified over time, with endophytes adapting to various plant lineages and environmental conditions, leading to the wide range of associations observed today. The shape of fungal endophytes was determined by a complex interplay of factors, including host plant characteristics, environmental gradients, geographical location, plant developmental stages, biotic interactions, anthropogenic effects, and climate change. Within plant tissues, fungal endophyte communities vary significantly, with roots, leaves, stems, and seeds hosting distinct assemblages influenced by their physiological and structural attributes. For example, root tissues are hotspots for DSE and AMF, while leaves are dominated by ascomycetes. Host plant genotype and phenotype further determine the diversity and composition of endophytes by providing specific chemical environments that foster colonization. Environmental factors such as temperature, humidity, soil type, and light availability critically shape fungal endophyte communities. Geographical and bio-geographical variables introduce further variation, with tropical regions exhibiting higher fungal diversity compared to temperate zones due to their favorable climatic conditions and host diversity. The distribution of endophytes is also influenced by developmental stages of plants, with older plants often hosting more diverse communities due to repeated colonization and structural changes in plant tissues. Biotic interactions with other microorganisms, including bacteria and mycorrhizal fungi, influence fungal endophyte dynamics, while human activities such as agriculture and deforestation alter local conditions, simplifying or disrupting endophyte communities. Moreover, climate change is driving shifts in fungal endophyte diversity as temperature and precipitation patterns evolve. Understanding these spatial distribution patterns provides insights into the ecological roles of fungal endophytes and their potential applications in sustainable agriculture and environmental conservation (Arnold et al. 2000).

2. Diversity of fungal endophytes and ecological functions

Endophytes are classified into two main groups: *clavicipitaceous endophytes* (C-endophytes), which primarily colonize grasses, and non-clavicipitaceous endophytes (NC-endophytes), found in a wide range of plants. While much research focuses on C-endophytes due to their agricultural importance, NC-endophytes are diverse and have distinct ecological roles Table 1 (Taylor et al. 2005; Rodriguez et al. 2009; Varanda et al. 2016; Chen et al. 2020; Sarkar et al. 2021).

C-endophytes (Class 1) are a small group of *clavicipitaceous* fungi primarily found in cool- and warm-season grasses, forming systemic infections within plant shoots. These fungi typically transmit vertically through seed infections and can enhance plant biomass and drought tolerance and provide herbivore resistance. Their effects depend on the host species and environmental conditions. NC-endophytes are highly diverse, spanning multiple fungal lineages and plant hosts, and are found in ecosystems ranging from the tropics to the tundra. They exhibit varied ecological roles and can alternate between endophytic and free-living states. NC-endophytes are categorized into three groups based on colonization patterns, transmission, and environmental functions. Class 2 endophytes can colonize both above- and below-ground tissues and confer habitat-specific stress tolerance, a unique trait among endophytes. The biodiversity and environmental roles of Class 3 and 4 endophytes are less well understood and may be revised as more research is conducted.

Table 1. Criteria for classifying fungal endophytic groups based on their symbiotic characteristics (Rodriguez et al. 2009; Wadhwa et al. 2024).

Criteria	***Clavicipitaceous***	***Non-Clavicipitaceous***		
	Class 1	**Class 2**	**Class 3**	**Class 4**
Host range	Narrow	Broad	Broad	Broad
Tissue(s) colonized	Shoot and rhizome	Shoot, root and rhizome	Shoot	Root
In planta colonization	Extensive	Extensive	Limited	Extensive
In planta biodiversity	Low	Low	High	Unknown
Transmission	Vertical and horizontal	Vertical and horizontal	Horizontal	Horizontal
Fitness benefits	NHA	NHA and HA	NHA	NHA

2.1. Clavicipitaceous endophytes (Class 1)

The *Clavicipitaceous* endophytes were first time identified in the late 19th century in the seeds of numerous grass species. Initial hypotheses proposed a link to toxic syndromes in animals ingesting infected tissues. However, these were not thoroughly examined until later, when *Neotyphodium coenophialum* was associated with the prevalent incidence of 'summer syndrome' toxicosis in cattle grazing on tall fescue pastures.

In 1988, Keith Clay posited that *Clavicipitaceous* endophytes serve as protective mutualists for host grasses (Nischitha 2024); this concept garnered considerable attention, prompting additional research into the natural history, evolution, ecology, and physiology of endophytes. The advantageous impacts of C-endophytes have prompted turfgrass breeders to introduce cultivars designated as 'endophyte enhanced.

Evolutionary Origins

The *Clavicipitaceae*, a family within the Hypocreales order of Ascomycota, encompasses both free-living and symbiotic species linked to insects, fungi, and various plants, including grasses, rushes, and sedges. The family is classified as a derived group within the Hypocreales order, recognized for encompassing plant pathogens, saprotrophs, and endophytes, many of which synthesize beneficial substances (Smith et al. 2013; Singh et al. 2017). Molecular sequence findings position several geographically widespread species in deeper evolutionary branches, indicating that saprobism was prevalent among early members of the family. Reconstructions of ancestral states suggest that *Clavicipitaceous endophytes* probably originated from insect-parasitic forebears, diversifying via inter-kingdom host transitions. The evolution of endophytic *Epichloë/Neotyphodium* and *Balansia* is believed to have originated from free-living insect parasites that later adapted to an epibiotic, plant-associated biotrophic lifestyle. These fungi acquired plant nutrients by infecting and inducing necrosis in scale insects and whiteflies. Over time, the capacity to directly infect grass hosts developed, with certain types becoming epibiotic and others endophytic. This evolutionary trajectory demonstrates a direct route to biotrophy, circumventing the conventional progression from virulent plant diseases to endophytes. Endophytes originating from insect diseases presumably lacked the requisite enzymes or toxins to eliminate or decompose plant tissues, enabling their colonization of plants without hindrance from plant defense mechanisms (Xia et al. 2022). Nutrient-utilization research indicates that biotrophy and endophytism in this group entailed a decrease in enzyme functions, heightened dependence on plant-sourced nutrients, and the synthesis of secondary metabolites advantageous to the symbiotic relationship. The capacity of these endophytes to synthesize toxins that impact insects, and other animals may derive from the chemical repertoire employed by insect-parasitic species (Panwar et al. 2024), such as *Cordyceps*, which share precursors with the toxins generated by endophytes (Rodriguez et al. 2009; Leuchtmann et al. 2014).

Impacts on host plant fitness

Many *clavicipitaceous endophytes* contribute to increased resistance against insect herbivory. Studies indicate that both the stain of fungus and the plant's growth stage play a role in deterring insect feeding. Mutational studies have identified fungal metabolites, such as peramine, that protect plants from herbivory. Some Class 1 endophytes also exhibit anti-nematode activity. However, not all Class 1 endophytes confer resistance to herbivores or nematodes, underscoring the importance of evaluating native plants under natural conditions to determine the benefits of endophytes. Specific endophytes also deter mammalian herbivores. For instance, sleepy grass, a species native to the western United States, contains an endophyte that synthesizes lysergic acid amide. When horses ingest small amounts of these grass, they experience temporary drowsiness but recover within a few days. The prevalence of this endophyte and its alkaloid production vary by geographic region, while its influence on herbivory and plant fitness is shaped by host genotype, environmental factors, and the coevolution between the plant and endophyte. Similar patterns are observed worldwide. In South America, *Neotyphodium tembladerae* infects certain grass species, rendering some toxic to mammals. In Asia, *Neotyphodium gansuense* is found in drunken horse grass, which grazing animals tend to avoid. Recent research also suggests that even endophytes lacking toxicity can reduce herbivory, as plants containing ergot alkaloids are less frequently consumed by herbivores (Petroski et al. 1992; Rodriguez et al. 2009; Bamisile et al. 2018; Lee et al. 2021).

The impact on sensitivity and disease resistance

The resistant related and influenced by Class 1 endophytes remains largely unexplored. Some C-endophytes form bioactive compounds that inhibiting the growth of fungi under laboratory conditions. For example, *Epichloë festucae* has been found to generate several antifungal compounds (Fardella et al. 2022). However, establishing a direct link between in vitro fungal suppression and actual disease resistance in plants has been challenging. While infected turfgrasses have exhibited resistance to leaf spot pathogens, it is unclear whether this is due to antifungal metabolites produced by the endophyte, a defensive response from the host plant, competition among fungi, or physical barriers preventing pathogen colonization (Card et al 2021; Kuźniar et al. 2024).

Significance in plant ecophysiology

Regardless of potential drawbacks, Class 1 endophytes may contribute to improving plant ecophysiology by enhancing tolerance to abiotic stresses such as drought and heavy metal contamination. Some studies have shown that *Neotyphodium coenophialum* infection develops extensive root systems, improving a plant's ability to acquire moisture and nutrients (Rodriguez et al. 2009).

2.2. Class 2 endophytes

Class 2 endophytes comprise many species, all classified within the *Dikarya* (Ascomycota or Basidiomycota). The majority belong to Ascomycota, with a lesser fraction from Basidiomycota. Ascomycota species are limited to the *Pezizomycotina,* encompassing various different classes. Class 2 endophytes within Basidiomycota comprise several species from *Agaricomycotina* and *Pucciniomycotina*. Class 2 endophytes are distinct from other NC-endophytes in multiple aspects: they generally colonize roots, stems, and leaves; establish extensive infections within host plants; are disseminated through seed coats or rhizomes; exhibit low prevalence in the rhizosphere; confer both habitat-specific and non-habitat-specific fitness advantages; and typically demonstrate high infection rates (90-100%) in plants from high-stress environments. While not all instances in this section fulfil every condition, they conform to a sufficient number to warrant inclusion (Spatafora et al. 2017; Gakuubi et al. 2021).

Advantages from symbiotic associations

Certain Class 2 endophytes contribute to plant stress tolerance through symbiotic associations. For instance, *Curvularia protuberata* colonizes the tissue of nonembryonic *Dichanthelium lanuginosum*, a geothermal plant, enabling both the fungus and its host to endure temperatures as high as 65°C. Likewise, *Fusarium culmorum* inhabits *Leymus mollis*, allowing both organisms to thrive in high-salinity environments. These cases illustrate how specific endophytes assist plants in coping with abiotic stress by living within their tissues. Consequently, some Class 2 endophytes function as mutualists, supporting their hosts while securing nutrients for their own growth and reproduction and mitigating abiotic stress through symbiosis (Liu et al. 2018; Morsy et al 2020).

Endophyte-induced fitness advantages and environmental adaptations of plants

Class 2 endophytes predominantly enhance the biomass of host shoots and/or roots, presumably through the induction or biosynthesis of plant hormones. Various organisms offer protection against fungal pathogens, potentially through the production of secondary metabolites (Table 3), fungal parasitism, or the induction of systemic resistance. The protective effect against disease may result from pathogens being unable to compete with endophytes for nutrients or ecological niches. Some Class 2 endophytes can asymptomatically colonize various genetically distinct host species, offering habitat-specific fitness benefits. Research comparing different endophyte species in plants from geothermal soils, coastal beaches, and agricultural fields demonstrates that *Curvularia protuberata* enhances heat tolerance, *Fusarium culmorum* offers salt tolerance, and Colletotrichum species confer disease resistance. Field studies indicate that nonsymbiotic plants cannot withstand environmental stresses in their natural habitats without colonizing habitat-specific endophytes. The ability of these endophytes to confer stress tolerance in a habitat-specific manner appears to be an adaptive process characterized by the subspecies level (Rodriguez et al. 2008; White and Andow 2008; Grabka et al. 2022).

Stress Tolerance Mechanism

Class 2 endophytes frequently improve plant biomass facing stress, yet the cellular mechanisms behind the adaptation to stress are not well characterized. Some biochemical pathways linked to symbiotically mediated stress resilience include the prompt activation of defensive responses in plants harboring endophytes when exposed to pathogens. However, in the absence of pathogen exposure, these plants do not activate their defenses (Hardoim et al. 2015; Bastías et al. 2021). Under abiotic stress, Class 2 endophytes protect plants in ways that do not always correlate with common stress responses like osmolyte production or increased osmotic potential. For instance, symbiotic plants exhibit lower water consumption compared to nonsymbiotic plants, irrespective of the specific Class 2 endophyte involved, indicating that enhanced water use efficiency may play a more critical role in drought tolerance than osmolyte regulation. Overall, Class 2 endophytes substantially impact plant ecophysiology, facilitating rapid adaptation and survival in highly stressful environments (Singh et al. 2011).

2.3. Class 3 Endophytes

Class 3 endophytes are defined by their predominant or exclusive presence in above-ground plant tissues, horizontal transmission, localized infections, and the ability to confer either beneficial or detrimental effects on hosts without strict habitat specificity. They also display remarkable in planta biodiversity. This group includes *hyperdiverse* endophytic fungi (Kamel et al. 2020) associated with tropical tree leaves, as well as diverse fungal communities inhabiting above-ground tissues of nonvascular plants, seedless vascular plants, conifers, and both woody and herbaceous angiosperms across various biomes, from tropical forests to boreal and Arctic/Antarctic regions. Class 3 endophytes colonize photosynthetic and herbaceous tissues, as well as flowers, fruits, and asymptomatic wood and bark. Fungi with similar life histories, found in asymptomatic lichens, are termed 'endolichenic' fungi.

Class 3 endophytes demonstrate substantial diversity within individual host tissues, plant species, and populations. For instance, healthy leaves in lowland tropical forests often harbor multiple independent infections rather than systemic or extensive hyphal growth. The biomass produced by any specific infection is minimal, with each leaf exhibiting a densely packed mosaic of various endophyte species. In tropical forests, individual leaves can harbor up to one isolate per 2 mm² of leaf tissue and often contain numerous species. Leaves from the same tree can host markedly different communities of endophytic fungi. Individual plants can support numerous species, while species within their native ranges may be associated with thousands of species. The extensive varieties observed in certain tropical plants and regions extend beyond tropical environments; temperate and boreal communities also exhibit a remarkable richness of Class 3 endophytes. Species accumulation curves for boreal and Arctic endophytes exhibit non-asymptotic behavior, with more than 50 species identified from a sample of 280 isolates analyzed. Over 80 endophyte species have been identified in Juniperus communis in Switzerland, while 78 species were isolated from the leaves and twigs of *Quercus petraea* in Austria. Class 3 endophytes, while horizontally transmitted, are generally differentiated from pathogens linked to the same host species and epiphyllous fungi on the same leaves. The distinction between Class 3 endophytes and saprotrophic communities remains a topic of debate; however, evidence suggests that Class 3 endophytes include species absent from saprophytic decay fungi. Endophytes of Class 3 are infrequently isolated from seeds.

The significant diversity of Class 3 endophytes prompts enquiries into their ecological functions. Recent studies primarily emphasize the characterization of bioactive strains or the enumeration of species. At the same time, insufficient attention has been directed towards the ecological roles of these fungi in plants or their evolutionary implications for plant species. The presence of numerous phylogenetically diverse endophytic fungi (Lacerda et al. 2022) within a single host's foliage complicates the identification of overarching ecological patterns. Class 3 endophytes have been experimentally assessed for their costs and benefits on limited occasions, and infrequently within the framework of multiple environmental or biotic stressors.

These fungi have been associated with improved disease resistance, deterrence of herbivores, and modified responses to drought and other abiotic stressors; however, the quantity of experimental and life-history studies remains limited compared to the spectrum of Class 3 endophytes. There is a critical need for research that addresses the inherent intricacy of endophyte communities and incorporates multitrophic interactions. The investigation of hyperdiverse Class 3 endophytes is currently in a highly promising and dynamic stage, akin to the rapid expansion of research on mycorrhizal symbioses.

Ecological roles

The environmental functions of Class 3 endophytes are challenging to identify due to their significant diversity within individual hosts or host tissues, and these roles have remained mainly unexamined. Several studies have assessed the costs and benefits of infection by introducing Class 3 endophytes into plants cultivated under sterile conditions. Typically, plants infected with multiple Class 3 endophytes exhibit no significant alterations in growth rate, biomass accumulation, root: shoot ratio, or other quantifiable traits after inoculation in vivo. Research indicates that bark endophytes protect trees from Dutch elm disease, while varied endophyte communities can mitigate lesion development and leaf mortality induced by Phytophthora sp. in Theobroma cacao (Arnold et al. 2003; Martínez-Arias et al. 2021). While certain Class 3 endophytes adversely affect plant growth, others may provide mutualistic advantages, including disease resistance or deterrence of herbivores. The ecological roles of Class 3 endophytes are diverse, prompting scientific inquiries in contrast to the more limited diversity observed in Class 1 and Class 2 endophytes. When examining the ecology of Class 3 endophytes, it is crucial to consider the intricate ecological dynamics of plant–endophyte interactions, encompassing rhizosphere and phyllosphere fungi, bacteria, and herbivores. The discovery of entomopathogenic fungi as endophytes offers insights into symbiotic ecology that may have been overlooked without examining herbivore plant endophyte interactions. This example highlights the necessity of collecting baseline data regarding all endophytes' abundance, diversity, and host specificity to investigate their ecological significance. Numerous studies have emphasized the varied ecological functions and possible applications of Class 3 endophytes, a highly diverse group still inadequately researched (Chitnis et al. 2020; Ahsan et al. 2024).

2.4. Class 4 Endophytes

During investigations of ectomycorrhizal fungi, Melin identified a pigmented fungus ranging in color from brown to black related to terrestrial plant roots. He referred to these sterile, root-associated organisms as mycelium radicus astrovirens (MRA) (Melin 1922). MRA frequently co-occurred with mycorrhizal fungi and was subsequently labelled as "pseudomycorrhizal." Shortly thereafter, Peyronel documented associations between over 135 angiosperm species and darkly pigmented fungi within root tissues. These fungi are now termed "dark septate endophytes" (DSE) and categorized under Class 4 endophytes. Class 4 endophytes are functionally characterized by darkly melanized septa and their exclusive localization within plant roots. Predominantly ascomycetous, these fungi exhibit conidial or sterile forms and produce melanized structures such as inter- and intracellular hyphae and microsclerotia within root tissues. DSE display minimal host or habitat specificity, being reported in approximately 600 plant species, including nonmycorrhizal plants, across diverse ecological zones ranging from Antarctic and Arctic regions to tropical ecosystems. Frequently found in boreal and temperate forests, particularly in association with coniferous tree and shrub fine roots, these fungi are non-pathogenic, as evidenced by their prevalence on healthy roots. Within this context, DSE is broadly classified as endophytes, colonizing living plant tissues without overt adverse effects. Globally widespread and abundant, DSE is prevalent in high-stress environments, suggesting a significant role in plant ecophysiology. However, nearly a century after their discovery, their precise ecological functions remain elusive (Rodriguez et al. 2009; Terhonen et al. 2018; He et al. 2019).

Phylogenetic diversity, classification, and ecological potential

The comprehensive diversity of DSE species and their host plants remains poorly defined, necessitating extensive global studies of plant-DSE associations. Latitudinal surveys examining plant species from pole-to-pole reported DSE associations with 600 species spanning 320 genera and 100 families. Colonization studies involving five anamorphic taxa (*Chloridium paucisporum*, *Leptodontidium orchidicola*, *Phialocephala dimorphosphora*, *Phialocephala fortinii*, and *Phialophora finlandia*) under natural and experimental conditions revealed a broad host range, with some taxa colonizing over 20 species (Jumpponen and Trappe 1998).

DSE represents a taxonomically and ecologically intriguing group, yet their classification is fraught with ambiguity due to broad criteria. The primary criterion for DSE designation is the existence of darkly pigmented, asexual, endophytes with septate within plant roots. However, misclassification can occur, as dark-pigmented endophytes from other groups may be incorrectly labeled DSE. For instance, the Class 2 endophyte *Curvularia protuberata*, which enhances thermal tolerance to *Dicanthelium lanuginosum*, is morphologically similar but colonizes all plant tissues, not just roots (Rodriguez et al. 2008). To avoid misclassification, researchers must examine all plant tissues for fungal colonization and employ septa-specific dyes to identify fungal structures accurately. Furthermore, the asexual designation of DSE is problematic, as many taxa remain uncharacterized, with potential functional and ecological overlaps among soil fungi, saprophytic rhizoplane inhabitants, pathogenic fungi, mycorrhizal fungi, and endophytes. As demonstrated in laboratory studies, DSE transmission likely occurs horizontally, facilitated by mycelial fragmentation and conidial dispersal. While anamorph–teleomorph connections remain unidentified for most DSE, the probability of sexual Replication cannot be ignored. Detailed descriptions of root colonization by *P. fortinii*, a model DSE species, reveal colonization beginning with superficial hyphae forming a loose network on root surfaces, followed by intracellular and intercellular growth. These fungi may form densely packed, thick-walled cells within root cortical tissues, called microsclerotia or sclerotial bodies (Jumpponen and Trappe 1998; Mandyam and Jumpponen 2005).

Unveiling the role of class 4 endophytes

Despite significant advancements in understanding the ecological roles of Class 1-3 endophytes, the symbiotic functionality of Class 4 endophytes remains poorly explored. Taxonomic identification of DSE is a critical initial step, but broader questions regarding their evolutionary history, symbiotic roles, and ecological contributions must now be addressed. It has been proposed that DSE, akin to mycorrhizas, are multifunctional, potentially enhancing plant resistance to pathogens by limiting rhizosphere carbon and producing melanin-associated secondary metabolites toxic to herbivores (Mandyam and Jumpponen 2005). These traits may confer competitive advantages to DSE-associated plants. Simple experiments are essential to elucidate DSE biological functions, urging the scientific community to prioritize research on these enigmatic fungi. While their precise roles remain unknown, DSE's widespread distribution and associations with diverse plant roots underscore their likely importance in plant ecophysiology (Table 2) (Newsham 2011).

Conclusion

Fungal endophytes have been essential partners in the evolution of land plants, enabling their adaptation to terrestrial environments and promoting biodiversity. The continuous interplay between these symbionts and plants offers valuable insights into ecological and evolutionary processes. By leveraging these ancient relationships, we can address modern challenges in agriculture

Table 2. Bioactive compounds derived from endophytic fungi isolated from a diverse array of medicinal plants

Medicinal plant	Endophytic fungi	Product of Interest	Pharmacological Effects	References
Salvia miltiorrhiza	*Phoma glomerata* D14	Salvianolic acid (phenolic acid)	Cardiovascular and cerebrovascular protective	Rodriguez et al. 2009 ; Manganyi and Ateba, 2020
Catharantus roseus	*Fusarium oxysporum*, *Talaromyces radicus*, and *Eutypella* spp.	Vinblastin and vincristine (alkaloids)	Antitumor	Hashem et al. 2023 ; Bard et al. 2024
Coleus forskohlii	*Rhizoctonia bataticola*	Forskolin (alkaloid)	Glaucoma, antitumor, anti-HIV, cardiovascular protective	Sarkar et al. 2021
Macleaya cordata	*Fusarium proliferatum* BLH51	Sanguinarine (alkaloid)	Antibacterial, antihelmintic, antitumor, anti-inflammatory	Giauque et al. 2019
Cajanus cajan	*F. solani*, *F. oxysporum*, and *F. proliferatum*	Cajaninstilbene acid (stilbenes)	Antioxidant	Song et al. 2009 ; Nisa et al. 2015
Cajanus cajan	*Hypocrea lixii*	Cajanol (flavonoide)	Antitumor (lung cell carcinoma)	Aly et al. 2013 ; Nelson et al. 2020

Table 2. (Contd.)

Medicinal plant	Endophytic fungi	Product of Interest	Pharmacological Effects	References
Cephalotaxus hainanensis	*Alternaria tenuissima*	Homoharringtonine (alkaloid)	Antitumor (chronic myeloid leukemia)	Vincent et al. 2016 ; Huang et al. 2020
Cinchona ledgeriana	*Phomopsis*, *Diaporthe*, *Schizophyllum*, *Penicillium*, *Fomitopsis*, and *Arthrinium*	Cinchona alkaloids	Antiparasitic (malaria)	Harrison and Griffin, 2020 ; Gakuubi et al. 2021
Passiflora incarnata	*Alternaria alternata*, *Colletotrichum capsici*, and *Chryseobacterium taiwanense*	Chrysin (flavonoid)	Antitumor (hepatic carcinoma)	Aly et al. 2011 ; Ezeobiora et al. 2021
Fritillaria cirrhosa	*Fusarium redolens*	Peimisine; imperaline-3-β-D-glucoside (alkaloids)	Antitussive and expectorant	Toghueo et al. 2018 ; Ancheeva et al. 2020
Rhodiola rosea	*P. fortinii*	Salidroside; p-tyrosol (phenolic compounds)	Antioxidant	Cheng et al. 2018 ; Ming et al. 2023
Solanum nigrum	*Aspergillus flavus*	Solamargine (alkaloid)	Antitumor	Chouhan et al. 2022 ; Tao et al. 2022
Piper nigrum	*Colletotrichum gloeosporioides*	Piperine (alkaloid)	Antibacterial, antifungal, hepatoprotective, antipyretic, anti-inflammatory, anticonvulsant, insecticidal, and antioxidant	Elliott et al. 2022; Niazi et al. 2023; Elbakary et al. 2024; Yadav et al. 2025
Digitalis lanata Ehrh.	*Alternaria* spp., *Penicillium* spp., and *Aspergillus* spp.	Digoxine (glycoside)	Cardiotonic	Taylor et al. 2003 ; Farouk et al. 2024
Capsicum annuum	*A. alternata*	Capsaicin (alkaloid)	Cardiovascular protective and antitumor	Ling et al. 2020 ; Henning et al. 2021
Ginkgo biloba	*F. oxysporum* SY0056	Glinkolide B (terpenoid lactone)	Renal, cardiovascular, and respiratory protective	Lee and Chatterton, 2003 ; Bogas et al. 2022
Nerium indicum	*Geomyces* sp.	Vincamine (indol alkaloid)	Cardiovascular and cerebrovascular protective; acetylcholinesterase inhibitor	Palmer, 2010 ; Fernandes et al. 2015
Rheum palmatum.	*F. solani*	Emodin; rhein (anthraquinones)	Antibacterial, anti-inflammatory, and hepatoprotective	Russo et al. 2016 ; Toghueo et al. 2019
Forsythia suspensa	*C. gloeosporioides*	Philliryn (lignan)	Antioxidant, anti-inflammatory, antipyretic, and hypolipidemic	Wang et al. 2019

Table 3. Bioactive metabolites detected through gas chromatography-mass spectrometry (GC–MS) analysis of the fungal extracts (Zhao et al. 2011; Nwobodo et al. 2024).

S/n	**Name of compound**	**RT (min)**	**MW (g/mol)**	**Nature of compound**	**Percentage composition (%)**		
					Lasiodiplodia theobromae	***Curvularia lunata Bv4***	***Curvularia lunata* Eg7**
1	β-Myrcene	6.301	136	Monoterpene	ND	ND	0.33
2	Oxirane, (chloromethyl)-	6.496	92.5	Ether	0.39	ND	1.01
3	Benzene, 1,4-dichloro-	6.849	147	Aromatic hydrocarbon	1.79	ND	1.57
4	1,3-Cyclohexadiene, 1-methyl-4-(1-methylethyl)-	6.956	136	Monoterpene	ND	ND	0.70
5	p-Cymene	7.201	134	Monoterpene	ND	0.72	1.27
6	Oxalic acid, isobutyl nonyl ester	8.113	272	Carboxylic acid ethyl ester	10.44	1.99	ND
7	γ-Terpinene	8.160	136	Monoterpene	ND	1.32	4.02
8	Dodecane, 2,6,11-trimethyl	8.382	212	Alkane	ND	ND	3.58
9	Hexadecane	8.644	224	Alkane	1.68	ND	ND
10	Undecane, 3,7-dimethyl-	8.700	184	Alkane	4.80	ND	1.55
11	Heptadecane, 2,6,10,14-tetramethyl	8.958	296.6	Alkane	10.82	ND	14.57
12	Octane, 3,5-dimethyl-	9.120	142	Alkane	ND	ND	2.12
13	Decane, 2,3,5,8-tetramethyl-	9.178	198	Alkane	ND	ND	3.39
14	Tetradecane	9.339	198	Alkane	ND	ND	5.13
15	Undecane	9.806	156	Alkane	ND	ND	8.12
16	Decane, 2,4-dimethyl-	10.101	170	Alkane	6.32	3.82	2.64
17	Dodecane	12.262	170	Alkane	1.47	ND	1.86
18	Naphthalene	14.950	128	Phenolic	1.51	1.24	ND
19	Tridecane	15.109	184	Alkane	1.73	1.24	4.44
20	Cetene	17.625	224	Alkene	ND	ND	1.62
21	Humulene	19.243	204	Sesquiterpene	ND	0.27	ND
22	β-Cubebene	19.964	204	Sesquiterpene	ND	0.75	ND
23	Pentadecane	20.413	212	Alkane	ND	0.81	1.11
24	β-Bisabolene	20.678	204	Sesquiterpene	ND	2.52	ND
25	2,4-Di-tert-butylphenol	20.974	206	Phenolic	7.44	4.04	9.22
26	Z-8-Hexadecene	22.690	224	Alkene	2.65	ND	3.16
27	Piperine	28.803	285	Alkaloid	ND	1.29	ND
28	Pentadecanoic acid, 14-methyl-, methyl ester	29.561	256	Fatty acid	0.70	ND	ND

Table 3. (Contd.)

S/n	Name of compound	RT (min)	MW (g/mol)	Nature of compound	Percentage composition (%)		
					Lasiodiplodia theobromae	***Curvularia lunata Bv4***	***Curvularia lunata* Eg7**
29	1-Octadecene	30.257	252	Alkene	3.18	ND	7.00
30	Hexadecanoic acid, ethyl ester	30.283	284	Fatty acid methyl ester	ND	5.54	ND
31	6-(Trifluoromethoxy)-N-(trimethylsilyl)-1,3-benzothiazol-2-amine	30.433	234	Benzothiazole	ND	ND	0.60
32	Palmitoleic acid	31.089	254	Fatty acid	ND	0.39	ND
33	Linoleic acid ethyl ester	31.629	308.5	Fatty acid ester	ND	4.05	ND
34	9-Octadecenoic acid, ethyl ester	31.662	310.5	Fatty acid ester	ND	3.35	ND
35	Ethyl Oleate	31.666	310.5	Fatty acid ester	0.56	ND	0.50
36	1-Docosene	31.814	308.6	Alkene	2.05	ND	2.17
37	Tetradecanoic acid, 2-hydroxy-, methyl ester	34.216	258	Fatty acid ester	ND	ND	1.11
38	9,19-Cyclolanost-24-en-3-ol, (3.beta.)	35.582	468.8	Alcohol	ND	ND	2.11
39	2-Methyl-Z,Z-3,13-octadecadienol	35.880	280.5	Alcohol	ND	0.48	ND
40	5. α-Cholest-8-en-3-one, 14-methyl-	36.021	398.7	Ketone	ND	ND	2.23
Total number of compounds identified					16	17	27

Where ND denotes the absence of detection for the specified compound within the fungal crude extract.

, conservation, and climate resilience. Advances in molecular biology have revealed the genetic and biochemical mechanisms underpinning endophyte-plant interactions, highlighting their potential applications in sustainable agriculture, climate adaptation, and ecosystem restoration. As environmental changes continue to shape plant-fungal dynamics, understanding these ancient partnerships offers valuable insights into plant evolution and resilience. These Recent advances in molecular biology and omics tools could illuminate the mechanisms underpinning fungal endophyte-plant interactions and highlight the intricate co-evolutionary dynamics of fungal-plant partnerships.

Conflict of interest

The authors declare that they have no conflict of interest.

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