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Endophytic fungi: Tracing the evolutionary roots and exploring the diversity of plant-fungal symbioses

Hu Y[1], Wei GY[1], Wen JT[1], Chang LF[1], Chen YS[1], Wang Y[2] and Nizamani MM[2*]

[1]*Guizhou Provincial Tobacco Company Guiyang City Company, Guiyang 550004, P.R. China*
[2]*College of Agriculture, Key Laboratory of Agricultural Microbiology of Guizhou Province, Guizhou University, Guiyang, Guizhou 550025, China*

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Abstract

The endophytic lifestyle, characterized by a symbiotic relationship between fungi and their host plants, is pervasive throughout the fungal kingdom. However, the question of whether all fungi have ancestors with endophytic lifestyles remains a topic of ongoing debate. This review paper aims to explore this question by examining the evolutionary history of endophytism in fungi, the diversity of endophytic fungi, and the ecological and host-specific factors that have influenced the evolution and diversification of endophytic lifestyles. While it is clear that not all fungi descend from endophytic ancestors, the prevalence and diversity of endophytism across the fungal phylogeny suggest that this lifestyle has evolved multiple times in response to various ecological and host-specific pressures. Future research, integrating modern genomic tools and experimental approaches, will likely shed more light on the complex evolutionary trajectories of endophytic fungi, and potentially contribute to applications in agriculture, industry, and medicine.

Keywords – Endophytic Ancestors – Evolution – Fungal – Phylogeny – Plant Interactions

Introduction

Fungi are a fundamental part of the Earth's biosphere, contributing significantly to nutrient cycling, promoting plant growth, and influencing ecological interactions (Rodriguez et al. 2009, Hawksworth & Lücking 2017, Harrison & Griffin 2020). The kingdom Fungi presents a stunning diversity of lifestyles, extending from saprophytic decomposers and plant or animal pathogens to beneficial symbionts in mutualistic relationships (Berbee et al. 2017, Lücking et al. 2020). A particularly intriguing aspect within this broad spectrum is the endophytic lifestyle, characterized by fungi colonizing plant tissues without causing evident harm to the host (Porras-Alfaro & Bayman 2011, Hardoim et al. 2015). Notably, these endophytes often provide substantial benefits to their hosts, such as facilitating nutrient acquisition, promoting growth, and bolstering defenses against pathogens (Arnold et al. 2003, Singh et al. 2011, Trivedi et al. 2021).

Despite the considerable knowledge accumulated about endophytes, the question remains: did all fungi originate from endophytic ancestors? The premise behind this inquiry stems from the pervasive presence of endophytes across the fungal phylogeny (Rodriguez et al. 2009, Hyde et al. 2019, González-Teuber et al. 2020). Endophytes are not restricted to a single taxonomic group; they

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Corresponding Author: Mir Muhammad Nizamani – e-mail – mirmohammadnizamani@outlook.com

span multiple diverse lineages (Grünig et al. 2008, Porras-Alfaro & Bayman 2011). This widespread prevalence suggests that endophytism might have been an inherent characteristic of the early fungal lineages that initially colonized terrestrial environments in tandem with the first plants (Arnold et al. 2003, Selosse et al. 2018, Field & Pressel 2018).

Exploring the evolutionary origins of endophytism offers valuable insights into the nature of initial fungal-plant interactions and the subsequent diversification of fungi into their present array of lifestyles (Rodriguez et al. 2009, Tedersoo et al. 2014, El Mansy et al. 2020). Moreover, such investigations could illuminate how a variety of ecological and evolutionary pressures have steered the transitions to and from endophytism (Porras-Alfaro & Bayman 2011, Giauque & Hawkes 2013). This review embarks on a deep dive into this captivating subject, scrutinizing both traditional and contemporary research from mycology, plant biology, and evolutionary biology, with the goal of better understanding the intricate network of fungal evolutionary relationships and the potential ancestral role of endophytism.

2. Fungal Phylogeny and the Evolution of Endophytism:

2.1. Overview of Fungal Phylogeny:

Fungi constitute a diverse and ubiquitous group of eukaryotic organisms, occupying nearly every ecological niche and performing roles as decomposers, mutualists, and pathogens, thereby contributing significantly to global ecosystem functions (Blackwell 2011, Hawksworth & Lücking 2017). Based on a combination of morphological, physiological, biochemical, and DNA sequence criteria, fungi are classified into several major phyla, namely *Chytridiomycota*, *Zygomycota*, *Ascomycota*, *Basidiomycota*, and *Glomeromycota* (James et al. 2006, Spatafora et al. 2016).

Chytridiomycota, or *chytrids*, considered to be among the most ancestral fungi due to their unique feature of flagellated spores, predominantly inhabit aquatic environments (Berbee & Taylor 2010). Certain species within this group have garnered attention for their role in the worldwide decline of amphibian populations (Berger et al. 1999, Voyles et al. 2009). Members of the *Zygomycota* phylum are mostly terrestrial, with the bread mold Rhizopus being a notable decomposer contributing to nutrient cycling (Kendrick 2017, Gryganskyi et al. 2018).

Ascomycota, colloquially known as the sac fungi, constitute the largest phylum within the fungal kingdom, hosting a vast array of yeasts, molds, and lichens (Kendrick 2017, Lücking et al. 2020). Within this group resides the model organism *Neurospora*, which has significantly contributed to genetic research, as well as the gastronomically prized truffles and morels (Clay & Holah 1999, Stensrud et al. 2007, Baptista-Ferreira et al. 2015). The *Basidiomycota* phylum encompasses commonly recognized mushrooms, toadstools, and puffballs, alongside notorious plant pathogens, including rusts and smuts (Hibbett et al. 2007, Kendrick 2017, Cao et al. 2021).

Glomeromycota are distinguished by their formation of symbiotic relationships with plants, aiding in nutrient acquisition, a relationship crucial to many ecosystems (Bonfante & Genre 2010, Smith & Read 2010, ud din Khanday et al. 2016). The study of fungal phylogeny remains a vibrant and ever-evolving field, with novel data consistently contributing to and refining our understanding of their complex evolutionary relationships (Hibbett & Taylor 2013, Tedersoo et al. 2018, Harrouard et al. 2022).

The phylogeny of fungi has been a subject of intense study and discussion, with molecular techniques, particularly DNA sequencing, significantly improving our understanding of fungal evolution and diversity (James et al. 2006). New groups continue to be discovered and our understanding of the relationships and classifications within the fungi kingdom is constantly evolving. Some fungi, however, do not neatly fit into these major categories and are classified as "incertae sedis", reflecting the lack of sufficient characteristic features or conflicting data (Spatafora et al. 2016).

2.2. The Evolution of Endophytism in Fungi:

Endophytism, the ability of specific fungi to reside within plant tissues without causing overt harm, is a widespread feature in the fungal kingdom. This trait has seemingly evolved multiple times across various lineages, suggestive of convergent evolution (Saunders et al. 2010, Rodriguez et al. 2009, Naranjo-Ortiz & Gabaldón 2019). The two most species-rich fungal phyla, *Ascomycota* and *Basidiomycota*, comprise numerous endophytic species (Arnold et al. 2007, Rodriguez & Redman 2008, Wijayawardene et al. 2022). The emergence of endophytism is proposed to have been intimately tied to the evolution of terrestrial plants, with fungi playing a crucial role in facilitating plant colonization of land by augmenting nutrient acquisition and resilience against environmental stresses (Selosse & Le Tacon 1998, Rodriguez et al. 2009, Raghuwanshi 2018).

There's a strong hypothesis suggesting that many endophytic fungi originated from pathogenic ancestors. Through evolutionary time, these fungi might have evolved less aggressive strategies to prevent the extinction of their hosts, thereby establishing a more sustainable, long-term association (Arnold et al. 2003, Arnold et al. 2009, Saunders et al. 2010). This transition from pathogenicity to endophytism might reflect a cost-benefit trade-off for the fungus: inhabiting plant tissue provides a protected environment and consistent nutrient supply, but requires the fungus to regulate its growth and virulence factors to avoid causing damage to the host (Rodriguez et al. 2009, Postma et al. 2015).

Advancements in genomic research have provided invaluable insights into the evolution of endophytism among fungi. Such studies have revealed that endophytic fungi often possess genes associated with plant cell wall degradation, signaling pathways, and secondary metabolite production, all of which are critical for their interactions with host plants (Gao et al. 2011, Knapp et al. 2012, Venice et al. 2020). Despite the substantial progress in understanding the evolutionary trajectory of endophytism in fungi, numerous questions remain unanswered. These include the specific mechanisms facilitating the transition from pathogenicity to endophytism, the role of the host plant in this transition, and how environmental variables might influence this process (Arnold et al. 2003, Schulz & Boyle 2005, Mattoo & Nonzom 2021).

2.2. Early Fungal-Plant Interactions and the Rise of Endophytism:

The earliest known evidence of fungi, inclusive of those associated with plants, hails from the Late Ordovician period, approximately 450 million years ago (Taylor & Osborn 1996; Heckman et al. 2001, Field et al. 2015). The pioneering terrestrial environments were contemporaneously colonized by both fungi and plants, though the nature of these initial interactions remains a topic of ongoing debate (Remy et al. 1994, Heckman et al. 2001, Lutzoni et al. 2018). Multiple theories exist concerning this issue: certain scholars propose that ancient fungi were largely saprophytic, dependent on decomposing organic material for their nourishment, exemplified by numerous species of *Mucor*. In contrast, other scientists postulate that primordial fungi were more inclined towards mutualistic relationships, such as the mycorrhizal partnerships often seen in *Glomeromycota*, presenting this as the prevailing norm (Smith & Read 2010, Andrews & Andrews 2017, Lehnert et al. 2017).

The fossil record for endophytic fungi is thin, largely due to their microscopic size and the inherent difficulty in preserving their delicate structures (Taylor et al. 2015). However, indirect evidence, such as the prevalence of mutualistic symbioses in early land plants, points towards the existence of endophytic relationships (Selosse & Le Tacon 1998). Additionally, certain paleobotanical studies have unearthed evidence of fungal structures within plant fossils, resonating with contemporary endophytes (Taylor 2005, Strullu-Derrien et al. 2014, Mitchell 2021).

The evolution of endophytism is widely viewed to have involved transitions from other lifestyles, most notably saprotrophy and pathogenicity. Certain fungi might have originally colonized plants as pathogens or saprotrophs, subsequently evolving into endophytes (Arnold et al. 2003, Rodriguez et al. 2009, Stone & Bidochka 2020). On the other hand, certain endophytes such as those from the genus *Fusarium*, may represent primitive or original states, with adaptations to different modes of existence evolving subsequently. The complexity of the data points towards numerous transitions between these modes of existence in the course of the evolutionary history of fungi (O'Donnell et al. 2000, Redman et al. 2001, Naranjo-Ortiz & Gabaldón 2019).

Despite the origins of endophytism remaining ambiguous, it's clear that endophytic lifestyles have evolved numerous times across a broad spectrum of fungal lineages. This suggests that endophytism offers considerable benefits that have enabled its recurrent evolution (Arnold et al. 2003, Rodriguez et al. 2008, Schardl et al. 2004, Selosse et al. 2018).

3. Endophytic Lifestyles across the Fungal Tree of Life:

3.1. Diversity of Endophytic Fungi:

Endophytic fungi comprise an exceptionally diverse cohort, spanning numerous phyla and genera throughout the fungal kingdom, and mirroring the vast array of host plants and ecosystems where these organisms are discovered (Arnold et al. 2007, Unterseher et al. 2011). These fungi have been identified in virtually all plant species examined, from grasses and herbs to shrubs and trees, encompassing both angiosperms and gymnosperms (Rodriguez et al. 2009, Hyde et al. 2019). Moreover, they are ubiquitously present across various ecosystems, from the lush tropical rainforests to arid deserts, and from flat lowland plains to high-altitude alpine environments (Arnold et al. 2007, Porras-Alfaro & Bayman 2011, Lehnert et al. 2017, Harrison & Griffin 2020).

Endophytes display remarkable taxonomic diversity, being discovered in the two primary divisions of the fungal kingdom – *Ascomycota* and *Basidiomycota*, as well as, albeit to a smaller extent, in other phyla (Arnold et al. 2000, Rodriguez et al. 2009, Naranjo-Ortiz & Gabaldón 2019). Within the *Ascomycota* group, the classes Dothideomycetes, Sordariomycetes, and Eurotiomycetes are particularly known for hosting a significant number of endophytic species, while within *Basidiomycota*, endophytes are frequently found in the class Agaricomycetes (Gazis & Chaverri 2010, Sheng-Liang et al. 2014, Dong et al. 2021).

The diversity of endophytic fungi extends beyond taxonomy, they also demonstrate a broad range of interactions with their host plants (Saikkonen et al. 1998, Rodriguez et al. 2009). Endophytes like *Penicillium resedanum* and *Piriformospora indica*, found within the tissues of desert plants, maintain a purely symbiotic relationship with their hosts. These endophytes assist the plants in acquiring essential nutrients from the harsh desert soil, stimulate their growth by producing hormones, and provide an innate defense mechanism against potential diseases (Verma et al. 1998, Rodriguez et al. 2009, Suryanarayanan et al. 2012). Conversely, others may function as latent pathogens, residing within host tissues and causing no harm until the host undergoes stress or becomes compromised (Saikkonen et al. 1998, Arnold et al. 2003).

Certain endophytes may display a range of interactions with their host plants, varying from mutualistic to neutral or even pathogenic, depending on environmental conditions (Saikkonen et al. 1998, Faeth & Fagan 2002, Schulz & Boyle 2005). This remarkable diversity, in terms of both taxonomy and ecological interaction, underscores the adaptable and flexible nature of endophytic lifestyles, suggesting that endophytism has had a crucial role in the evolution and diversification of fungi (Rodriguez et al. 2009, Van Bael et al. 2012, Bahram & Netherway 2022). The recurrent evolution of endophytism across diverse fungal lineages also suggests that there are significant selective advantages associated with this lifestyle (Márquez et al. 2007, Rodriguez et al. 2009, van Der Heijden et al. 2015, Knapp et al. 2018).

3.2. Evolutionary Transitions to and from Endophytism:

The widespread occurrence of endophytic lifestyles across the fungal tree of life suggests multiple evolutionary transitions to and from endophytism. The factors driving these transitions are likely multifaceted, involving both ecological and genetic influences. In this section, we explore the various evolutionary pathways by which fungi have transitioned into and out of endophytic lifestyles.

3.2.1. Transition from Saprotrophy to Endophytism:

The transition from a saprotrophic lifestyle, involving the consumption of decaying organic matter, to an endophytic lifestyle, characterized by living within plant tissues, is likely dictated by a multitude of complex factors. For example, Sebacinales, a saprotrophic fungus, can shift to an endophytic lifestyle under certain conditions (Zuccaro et al. 2011, Weiß et al. 2016). As shown in

Fig. 1, the transition from saprophytic to endophytic lifestyles in fungal species involves several key drivers.

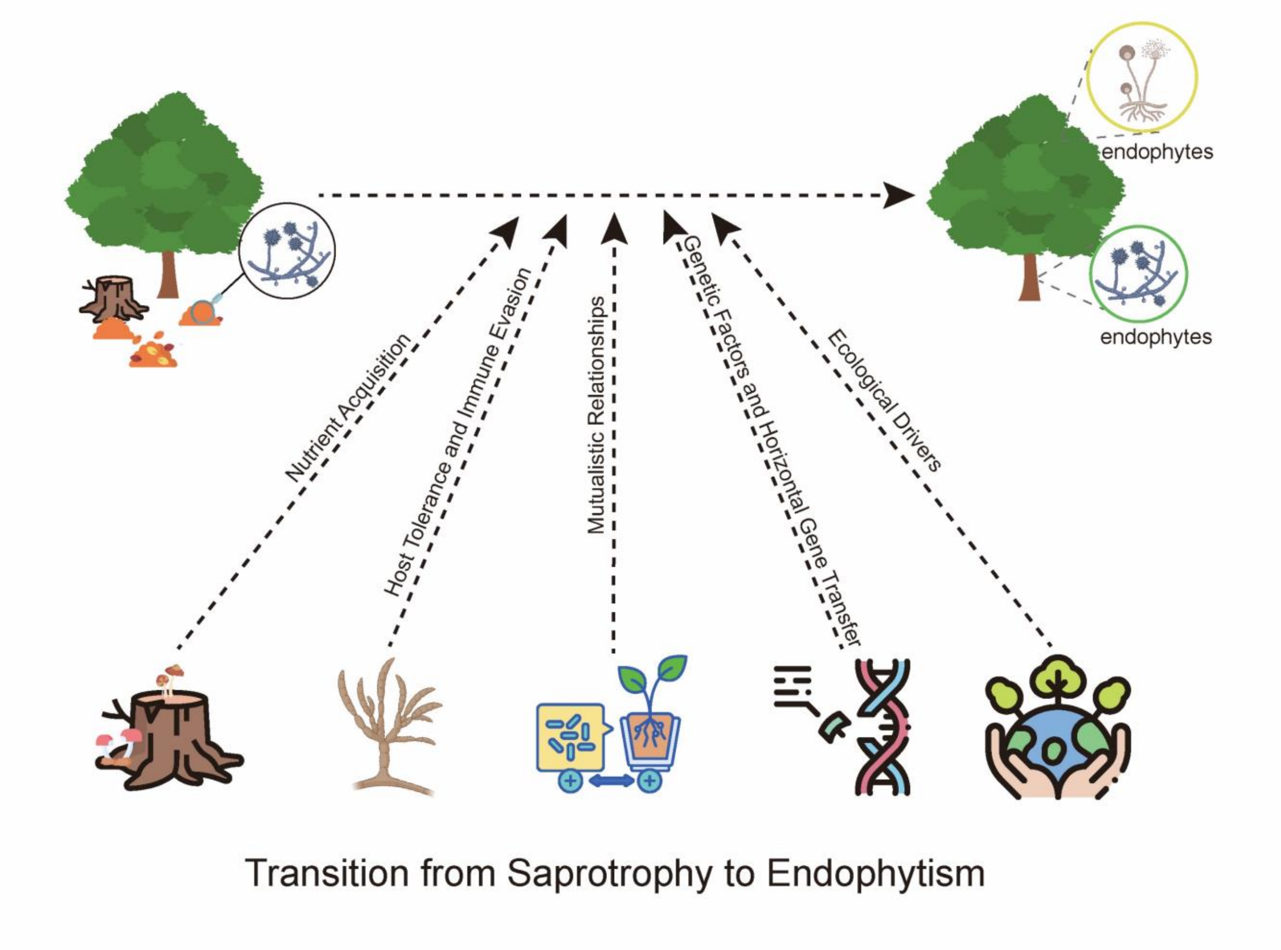

Fig. 1 – Drivers transition from saprophytic to endophytic lifestyles in fungal species.

(a) Nutrient Acquisition

The ability to degrade complex plant materials for nutrient acquisition is a key trait shared by saprotrophic and endophytic fungi, which can facilitate the transition between these lifestyles. Saprotrophic fungi, such as *Trichoderma reesei*, have evolved to decompose dead plant materials, breaking down complex organic molecules like cellulose and lignin to extract nutrients (Seiboth et al. 2011). They accomplish this feat using an array of enzymes, including cellulases that break down cellulose and ligninases that degrade lignin, the main components of the plant cell wall. This trait could have eased the transition of some saprotrophic fungi to an endophytic lifestyle, enabling them to derive nutrients from living plant tissues. For example, *Epichloë festucae*, a fungal endophyte, lives within the *Festuca pratensis* (Huds.) and *Festuca rubra* (L.) tissues, providing benefits to the host plant while receiving nutrients in return (Vikuk et al. 2019). The ability to access nutrients from both dead and living plant materials offers these fungi flexibility in adapting to different environments or host conditions, making them an interesting subject of study in the context of plant health and disease management.

(b) Host Tolerance and Immune Evasion

The successful colonization of living plant tissues by fungi requires sophisticated strategies to counteract the host's defensive responses. This involves a delicate balance of evading the plant's immune system while simultaneously establishing a stable relationship with the host (Kemen 2014). For instance, *Fusarium oxysporum*, a common fungal endophyte, is particularly adept at avoiding the plant’s immune response. Several studies have shown that *F. oxysporum* employs a range of techniques to evade the plant’s immune system. This includes the production of molecules called effectors that are able to suppress plant immunity and promote fungal colonization (Gladieux et al. 2015, Ma et al. 2010). Further, these effectors can interfere with the plant’s intracellular signaling pathways, which typically activate upon pathogen recognition and trigger immune responses. By disrupting these pathways, *F. oxysporum* hinders the activation of the plant’s defenses (Doehlemann et al. 2009).

However, in addition to active immune evasion, these fungal endophytes may also exploit host tolerance mechanisms. Tolerance, unlike resistance, does not directly limit pathogen growth but allows the host to endure the infection without substantial damage. The mechanisms of tolerance are not as well-studied as those of resistance but are believed to involve processes such as nutrient reallocation or repair of damaged tissue (Roy & Kirchner 2000). Moreover, tolerance to fungal endophytes may not be universal across all plant species or even among individuals of the same species, pointing to complex plant-endophyte interactions that are shaped by both host and microbial genetic factors (Saikkonen et al. 1998). The success of fungal endophytes like *F. oxysporum* in colonizing plant tissues is largely due to their capacity to evade or manipulate the host’s immune response and to potentially exploit host tolerance mechanisms.

(c) Mutualistic Relationships

Endophytic fungi, which colonize the internal tissues of plants without causing apparent disease, are recognized for their ability to cultivate beneficial mutualistic relationships with their host plants over time. For instance, the endophyte *Neotyphodium coenophialum* is known for establishing such relationships (Hunt & Newman 2005, Rodriguez et al. 2009). *N. coenophialum*, like many other endophytes, can offer an array of advantages to the host plant. These benefits range from protection against pathogenic microorganisms and insect pests to enhanced nutrient uptake and resilience to environmental stressors. The protection from pests and pathogens often involves the production of bioactive compounds that deter herbivores and inhibit pathogen development (Hunt & Newman 2005).

Similarly, the facilitation of nutrient uptake often involves the endophyte’s capacity to access or mobilize nutrients from the environment more effectively than the host plant could alone. For instance, certain endophytes can aid in the uptake of phosphorus or nitrogen, critical nutrients for plant growth (Bücking & Kafle 2015). The increased stress tolerance mediated by endophytes can manifest in several ways, including an enhanced ability to withstand drought, extreme temperatures, or high salinity. This attribute is particularly valuable in the context of changing environmental conditions associated with climate change (Rodriguez et al. 2008).

This type of mutualistic relationship is also exhibited by the ergot fungus, *Claviceps purpurea*, which produces alkaloids that can protect the host plant against herbivorous insects. While these alkaloids can be harmful to animals, including humans, they provide a clear benefit to the plant by reducing herbivore damage (Wäli et al. 2013). Endophytic fungi like *N. coenophialum* and *C. purpurea* have evolved a sophisticated mutualistic relationship with their host plants, offering a suite of benefits in exchange for a protected, nutrient-rich environment in which to proliferate (Schardl et al. 2004, Wäli et al. 2013).

(d) Genetic Factors and Horizontal Gene Transfer

The transition to and subsequent evolution of endophytic lifestyles in fungi are complex processes likely driven by a multitude of genetic modifications. These can range from point mutations to larger-scale genomic changes such as gene duplications or losses. Collectively, these modifications can equip endophytic fungi with the traits necessary to survive within a plant host, including the ability to evade or suppress host defenses and to extract nutrients from plant tissues (Hardoim et al. 2015). In the case of *Aspergillus* species, for example, studies have revealed significant genetic variations that could have contributed to the adaptation to endophytic lifestyles. These variations might involve alterations in genes that regulate immune evasion, nutrient uptake, or interactions with the plant host (Rosewich & Kistler 2000, Gladieux et al. 2014).

Moreover, horizontal gene transfer (HGT) – the transfer of genetic material between organisms that are not parent and offspring - can play a pivotal role in this evolutionary process. By acquiring genes from other organisms, fungi can rapidly gain new capabilities. This phenomenon has been documented in several fungal lineages, including *Penicillium* species (Richards et al. 2009). In *Penicillium*, evidence for HGT has been found in the form of genes likely acquired from bacteria. These transferred genes can provide diverse functions, potentially contributing to the fungi's ability to adapt to life within plant tissues. For instance, genes involved in detoxification of plant defense compounds or in the synthesis of growth-promoting hormones have been identified as possible results of HGT (Wisecaver et al. 2014). Taken together, these findings underscore the significant role of genetic factors and mechanisms such as HGT in the evolution of endophytic lifestyles in fungi. These elements collectively shape the complex and dynamic interactions between endophytic fungi and their plant hosts.

(e) Ecological Drivers

Ecological pressures are critical forces that drive the evolution and diversification of species, influencing their behaviors, traits, and interactions with the environment. Fungi, including those adopting an endophytic lifestyle, are no exception to this rule. Factors such as competition for resources, changes in environmental conditions, and pressures from predators or pathogens can spur significant evolutionary changes (Hardoim et al. 2015). In particular, the transition to an endophytic lifestyle – where fungi inhabit plant tissues without causing apparent harm – could be driven by intense competition in the fungi's native environments. As soil-dwelling fungi compete for limited resources such as nutrients and space, those capable of colonizing plants could gain a significant advantage by accessing a new, relatively unexploited niche (Saikkonen et al. 1998).

Rhizoctonia solani, a widespread soilborne fungus, is known to adopt both pathogenic and endophytic lifestyles. Its transition to endophytism could have been influenced by the competitive pressures in its native soil ecosystem. By entering plant tissues, *R. solani* could evade competition and access the nutrients available within the plant, effectively exploiting the host as a novel habitat (Arnold et al. 2003, Nguyen et al. 2016). Similarly, environmental changes, such as alterations in climate, can also shape the evolution of endophytic lifestyles. Endophytes may be more resilient to environmental stressors such as drought or temperature extremes compared to their free-living counterparts, as the plant host can offer protection and stable conditions (Redman et al. 2002). Ecological pressures, including competition and environmental changes, play a pivotal role in driving the shift of fungi like *R. solani* to endophytic lifestyles. These ecological drivers highlight the dynamic and adaptive nature of fungal-plant interactions, contributing to the diversity and complexity we observe in nature today.

The transition from a saprotrophic to an endophytic lifestyle entails considerable adaptations and is likely influenced by a blend of ecological pressures and genetic factors (Berbee & Taylor 2010, Schulz & Boyle 2005, Nguyen et al. 2016). As in the case of the fungus *Beauveria bassiana*, gaining insights into these transitions can elucidate the evolution of symbiotic relationships and the factors that determine microbial community structure and function (Saikkonen et al. 1998). As evidenced in certain fungal species, the transition from a saprophytic to an endophytic lifestyle involves significant adaptations and reveals the complexity of this evolutionary process. Table 1 below highlights fungal species and describes their shift from saprophytic to endophytic lifestyles.

3.2.2. Transition from Pathogenicity to Endophytism:

Endophytic fungi likely represent a broad spectrum of evolutionary histories, with some evolving from plant pathogens. This transition from a pathogenic to an endophytic lifestyle likely involves a reduction in virulence. As shown in Fig. 2, the transition from pathogenic to endophytic lifestyles in fungal species involves several key drivers. The information presented in Table 2 is based on the pathogenic and endophytic roles of selected fungal species.

(a) Reduced Virulence and Long-Term Association

Fungal pathogens can also have complex relationships with their plant hosts, often driven by similar pressures to reduce virulence and maintain a long-term association (Rodriguez et al. 2009).

Table 1 Transition from saprophytic to endophytic lifestyles in fungal group.

Organism	Transition Description	References
Alternaria spp.	Primarily saprophytic, but can transition to an endophytic lifestyle based on environmental factors and host availability.	DeMers (2022)
Aspergillus spp.	Aspergillus species are known for their saprophytic lifestyle, but they can also exist as endophytes in plants, potentially providing benefits to the host.	Zhang et al. (2018), Hagag et al. (2022)
Pestalotiopsis spp.	Reported as saprophytic, can also transition to an endophytic lifestyle.	Guba (1961), Maharachchikumbura et al. (2011)
Phomopsis spp.	Exhibits a variety of lifestyles, including saprophytic and endophytic; switches depending on environmental conditions.	Udayanga et al. (2011), Zhou et al. (2017), Zhou et al. (2018)
Piriformospora indica	Likely transitioned from a saprophytic to an endophytic lifestyle; aids in plant growth and disease resistance.	Zuccaro et al. (2011)

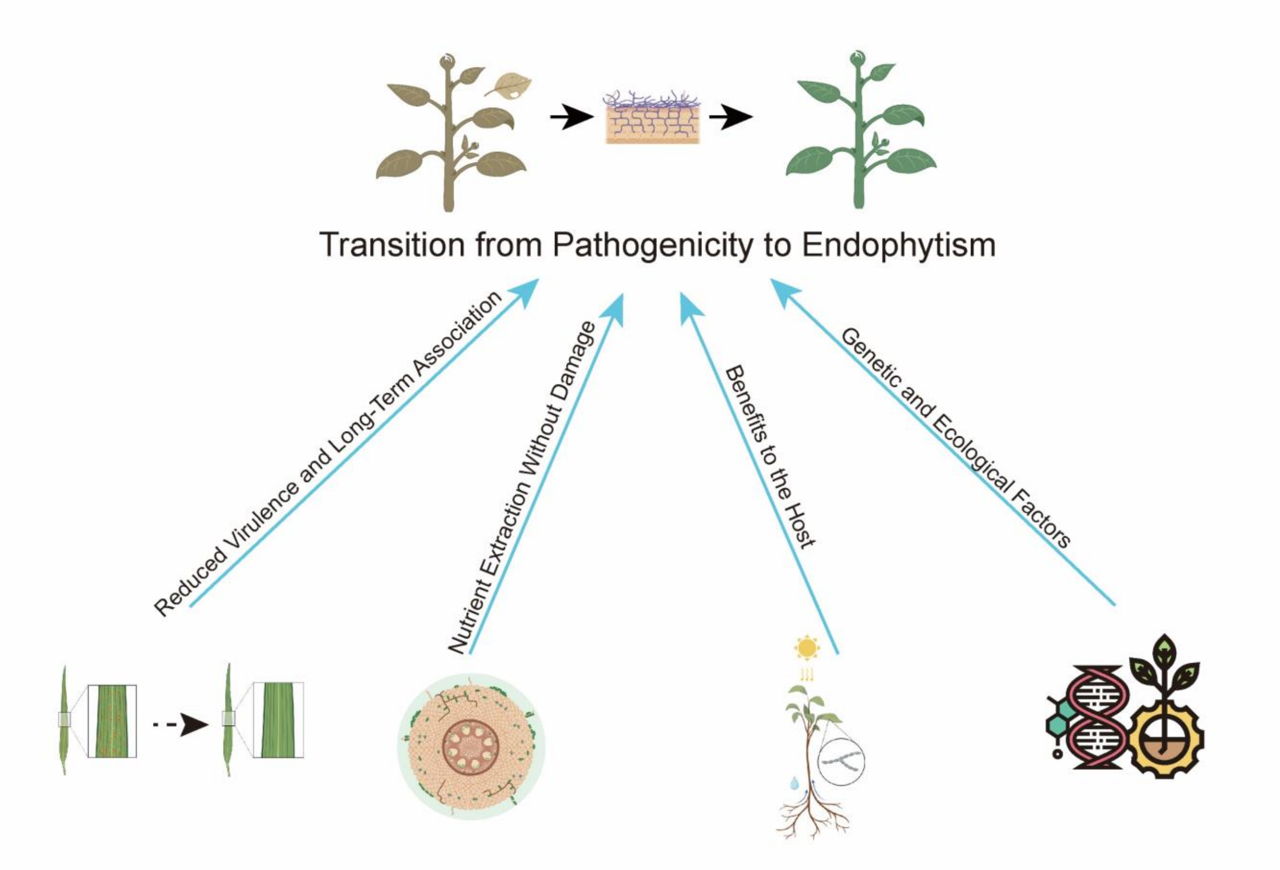

Fig. 2 – Drivers transition from pathogenic to endophytic lifestyles in fungal species.

Table 2 Pathogenic and endophytic roles of selected fungal group.

Fungus	Pathogenic role	Endophytic role
Alternaria spp.	Known for causing leaf spot and other diseases in a wide range of plants (Hou et al. 2016)	Strains can exist as endophytes without causing noticeable disease symptoms (DeMers 2022)
Aspergillus spp.	Common in soil and can cause a range of plant diseases (Paulussen et al. 2017)	Found as endophytes in a variety of plant species (Hagag et al. 2022)
Beauveria bassiana	Insects' pathogen, used as a biological control agent (Ortiz-Urquiza & Keyhani 2016)	Can exist as an endophyte in various plants, providing protection against certain pests (McKinnon et al. 2017, Barra-Bucarei et al. 2019)
Botryosphaeria dothidea	Causes white rot and cankers in a wide range of host plants (Ding et al. 2017, Marsberg et al. 2017)	Can exist as an endophyte in numerous plant species (Smith et al. 1996, Xiao et al. 2014)
Botrytis cinerea	Well-known plant pathogen causing grey mold (Tarkowski et al. 2019)	Strains can exist as endophytes without causing noticeable disease symptoms (Van Kan et al. 2014)
Candida spp.	Causes candidiasis in humans and animals (Rodríguez-Cerdeira et al. 2020)	Found as commensals in the human microbiome (Romo & Kumamoto 2020)
Cercospora spp.	Causes leaf spot diseases in a variety of plants (Meghvansi et al. 2013, Sautua et al. 2020)	Strains exist as endophytes without causing symptoms (Feng et al. 2014, Mookherjee et al. 2020)
Colletotrichum spp.	Known for causing anthracnose diseases in many plant species (Cannon et al. 2012)	Can exist as endophytes, particularly in medicinal plants (Rai et al. 2014)
Diaporthe spp.	Causes stem canker and pod and stem blight in soybeans, fruit rot in a variety of crops (Zhao et al. 2022)	Known to also occur as endophytes in various plant species (Gomes et al. 2013, Huang et al. 2015, Chepkirui & Stadler 2017)
Fusarium oxysporum	Causes fusarium wilt in a wide range of plant species (Gordon 2017)	Strain can live as endophytes in healthy plants e.g., banana (Musa sp.), providing some level of protection against other pathogens (Waweru et al. 2014)
Mycosphaerella spp.	Causes leaf spot diseases in a variety of plants (Crous 1998, Hunter et al. 2011)	Strains may live as endophytes without causing harm (Ibrahim et al. 2017, de Oliveira et al. 2018)
Penicillium spp.	Species cause post-harvest decay in fruits and other crops (Abdullah et al. 2016, Habib et al. 2021)	Strains exist as endophytes, promoting plant growth (Waqas et al. 2012, Hassan 2017)
Phoma spp.	Common plant pathogens (Deb et al. 2020)	Can exist as endophytes in certain plant species (Hossain 2021)
Septoria spp.	Causes Septoria leaf spot, affecting many plant species (El-Gamal et al. 2021)	Strains may exist as endophytes in various plants (Hatamzadeh et al. 2020)
Taphrina deformans	Causes peach leaf curl (Cissé et al. 2013)	Can live endophytically during certain stages of its life cycle (Unterseher et al. 2007)
Trichoderma spp.	Species are known for causing green mold in mushrooms (Ospina-Giraldo et al. 1998, Shah et al. 2012)	Known for colonizing plant roots as endophytes and providing benefits to the host (Bailey & Melnick 2013, Tseng et al. 2020)
Verticillium dahliae	Causal agent of Verticillium wilt in a wide range of plant species (Wheeler et al. 2019)	Some strains live as endophytes in healthy plants (Wheeler et al. 2019)
Xylaria spp.	Some species cause root rot in orchids and other plants (Proffer 1988)	Known as endophytes in numerous plant species (Liu et al. 2008, Zhang et al. 2014)

(1) Rust Fungi (*Pucciniales*)

These fungi are among the most devastating pathogens of agricultural plants. However, many of these fungi have evolved to be host-specific and exhibit reduced virulence on their host plants (Aime et al. 2017). This reduction in virulence is crucial for their long-term association with the host. By being less virulent, they can persist on the host for extended periods without causing its death. This strategy enhances their own survival and facilitates their ability to spread and infect other susceptible plants.

(2) Endophytic Fungi

Endophytic fungi are another example of fungi that exhibit reduced virulence and establish long-term associations with their plant hosts. These fungi live inside plant tissues without causing apparent harm (Saikkonen et al. 1998). Fascinatingly, certain endophytes like *Trichoderma harzianum* have developed strategies to diminish the harmful impact of other pathogens that might infect the host plant. These endophytes can accomplish this by either outcompeting the pathogens for resources, analogous to survival of the fittest, or by provoking the host plant's immune responses, consequently offering a safeguarding effect (Harman et al. 2004).

(3) Powdery Mildew

These fungi are known to colonize the surfaces of plant leaves, stems, and fruits, forming a distinct white or grayish powdery coating (Glawe 2008). While these fungi can potentially cause damage to the host plants, particularly when present in high densities, many plants have developed a certain level of tolerance to powdery mildew infections without suffering severe harm. Certain plants, for instance, tomatoes (*Solanum lycopersicum*), show varied levels of resistance or capabilities to restrain the propagation and impact of fungi. They achieve this through different defense strategies, which include strengthening their cell walls, generating antimicrobial substances, or activating specific defense reactions, akin to the systemic acquired resistance observed in response to *Fusarium oxysporum* infections (Mandal et al. 2009). This allows the plants to tolerate a certain level of powdery mildew infection while maintaining their overall health and reproductive success.

(b) Nutrient Extraction Without Damage

Endophytic fungi that have evolved from pathogens maintain the capacity to penetrate plant tissues and extract nutrients, much like their pathogenic ancestors. However, these fungi would have likely undergone evolutionary changes to carry out nutrient extraction without inflicting significant damage to the host plant (Saikkonen et al. 1998). For example, certain endophytic fungi have been found to establish mutualistic associations with grasses. These fungi, which are descendants of pathogenic ancestors, reside within the plant tissues and facilitate nutrient uptake without causing harm to the host. In a study by Rodriguez et al. (2008), it was observed that the endophytic fungus *Epichloë festucae* enhances the nutrient status and growth of its grass host, but does not exhibit pathogenic effects.

(c) Benefits to the Host

Over time, the evolution of endophytic fungi from pathogens can lead to the development of various beneficial traits that further strengthen the symbiotic relationship with their host plants (Rodriguez et al. 2009). These benefits can enhance plant fitness, growth, and stress tolerance. Certain endophytic fungi, like the *Beauveria bassiana* in the opium poppy (*Papaver somniferum*), have been identified to boost plant resilience against herbivores or disease-causing agents (Quesada-Moraga et al. 2006, Quesada-Moraga et al. 2014). These fungi can generate substances that repel or hamper the growth of herbivores or pathogens, thereby serving as a protective shield for the host plant (Behie & Bidochka 2014a). Additionally, endophytic fungi can contribute to improved nutrient acquisition by enhancing the uptake and mobilization of essential elements, such as nitrogen or phosphorus, for the host plant (Chhabra & Dowling 2017). This can have positive effects on the overall growth and health of the plant. Furthermore, endophytic fungi may assist the host plant in coping with environmental stresses, such as drought, salinity, or high temperatures. They can produce enzymes or metabolites that help alleviate stress-related damage or enhance the plant's ability to tolerate adverse conditions (Rodriguez et al. 2009). By providing these benefits, endophytic fungi establish a mutually beneficial association with their host plants, promoting the plant's fitness and survival, while also ensuring their own persistence and transmission.

Arbuscular mycorrhizal fungi (AMF) exemplify a mutualistic association with various plant species. These fungi colonize the roots of plants and form structures called arbuscules, which allow for nutrient exchange between the fungus and the host plant. The fungal hyphae extend into the soil, greatly expanding the plant's root system and enhancing its capacity to absorb water and nutrients, particularly phosphorus (Smith & Read 2010). In return, the plant provides the fungi with carbohydrates produced through photosynthesis. This mutualistic relationship benefits both the fungi and the host plants by improving nutrient acquisition and promoting overall plant health.

(d) Genetic and Ecological Factors

The transition from a pathogenic to an endophytic lifestyle in fungi is a complex process that would involve genetic changes and be influenced by ecological factors. This transition requires significant adaptations to establish a mutually beneficial relationship with the host plant. Genetic changes are expected to play a crucial role in the evolution of endophytic fungi from their pathogenic ancestors. These genetic changes may involve alterations in gene expression, gene regulation, or the acquisition of new genes that facilitate the establishment of an endophytic lifestyle (Porras-Alfaro & Bayman 2011). For example, genes related to pathogenesis might be downregulated or modified to avoid host damage, while genes involved in nutrient acquisition or host interaction may be upregulated to support the symbiotic association. Ecological factors also come into play during this transition. The availability of suitable host plants and their specific traits may influence the selection and adaptation of fungal pathogens towards endophytic lifestyles. Environmental conditions, such as nutrient availability or competition with other microorganisms, can also shape the evolution of endophytic fungi (Porras-Alfaro & Bayman 2011). For instance, competition with other pathogens or microorganisms may favor the development of strategies that allow endophytic fungi to outcompete or inhibit their potential competitors. The transition from a pathogenic to an endophytic lifestyle represents an evolutionary process driven by genetic changes and ecological factors. Understanding these factors can provide insights into the mechanisms underlying the establishment and persistence of endophytic associations in fungi.

The transition from a pathogenic to an endophytic lifestyle involves a shift from a short-term, exploitative relationship to a long-term, often mutually beneficial symbiosis. This transition is likely driven by a combination of genetic and ecological factors, and can lead to the evolution of diverse endophytic fungi that play important roles in plant health and ecosystem functioning (Rodriguez et al. 2009).

3.2.3. Transition from Endophytism to Other Lifestyles:

The evolutionary pathways of endophytic fungi are not unidirectional, and they have the potential to transition to saprotrophic or pathogenic lifestyles. This versatility allows for dynamic changes in fungal interactions with their hosts and the surrounding environment. As shown in Fig. 3, the transition from endophytic to other lifestyles in fungal species involves several key drivers.

(a) Transition to Saprotrophy

Certain endophytic fungi, such as *Xylaria* species, possess the capability to shift to a saprotrophic lifestyle by invading and breaking down deceased plant tissues, thus playing a crucial role in nutrient recycling in ecosystems (Del-Prado et al. 2010). These fungi retain their capacity to degrade plant cell wall components, a trait acquired during their endophytic phase, which enables them to break down the complex structures of decaying plant material. The transition to saprotrophy, however, necessitates adaptations to the unique environmental conditions and microbial communities associated with decomposing plant matter. Saprotrophic fungi encounter different nutrient availability, competitive interactions, and physical conditions compared to endophytic fungi. They need to adjust their metabolic processes, enzyme production, and resource utilization strategies to effectively decompose dead plant tissues and compete with other saprotrophic organisms present in the decomposer community (Márquez et al. 2012). These adaptations may involve alterations in gene expression patterns, changes in enzyme production, or modifications in nutrient uptake systems to exploit the available resources in the decaying plant material. The transition to saprotrophy represents an evolutionary shift in lifestyle and the ability to utilize different ecological niches and substrates for growth and nutrient acquisition.

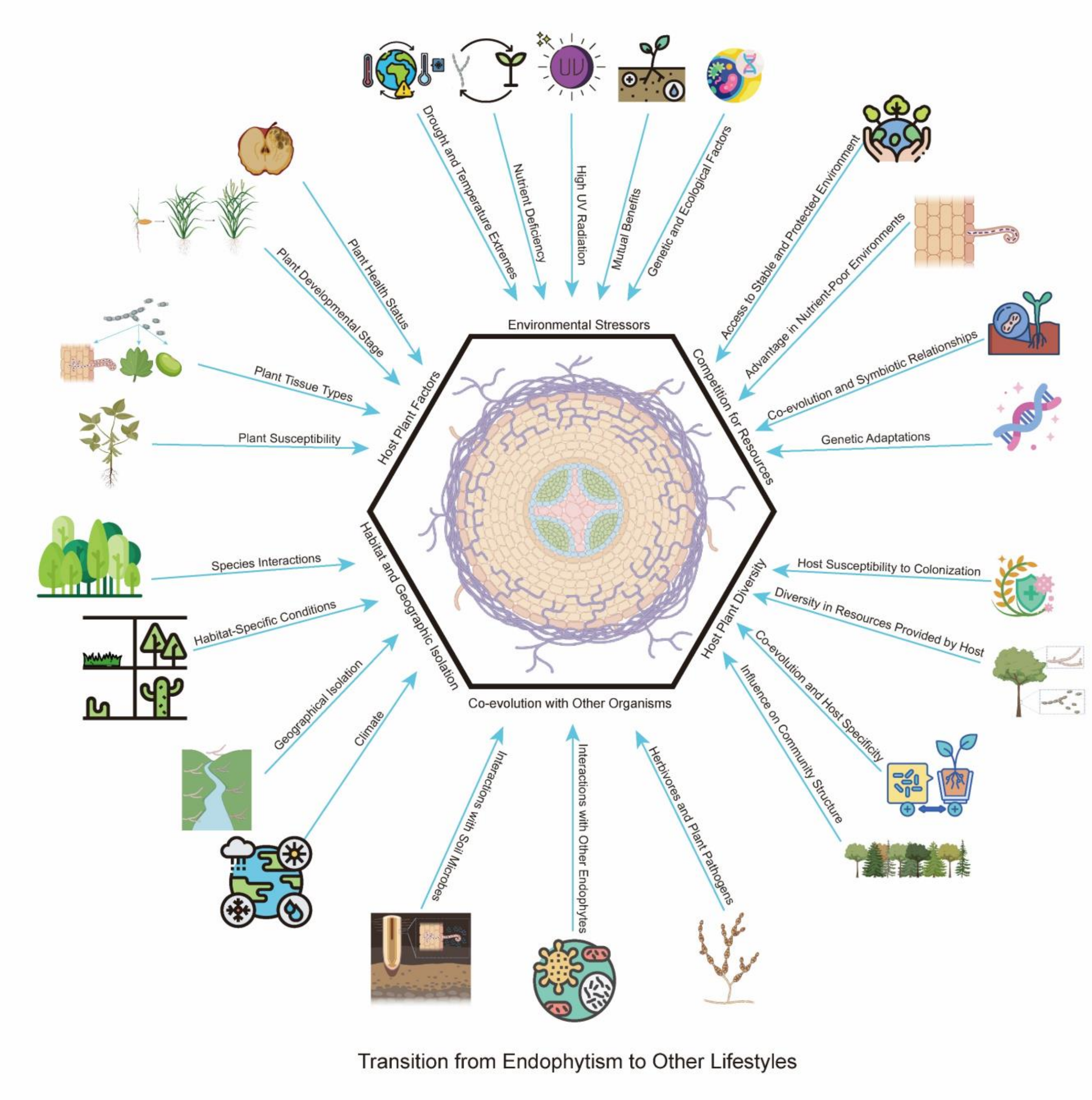

Fig. 3 – Drivers of transition from endophytic to other lifestyles in fungal species.

One example of an endophytic fungus that can transition to a saprotrophic lifestyle is the genus *Colletotrichum*. *Colletotrichum* species are known as plant pathogens causing anthracnose disease in various crops. However, certain *Colletotrichum* species can also establish endophytic associations with host plants. For instance, *Colletotrichum tofieldiae* is an endophytic fungus commonly found in grasses. In a study by Mousa et al. (2015), it was demonstrated that under certain conditions, *C. tofieldiae* can shift from an endophytic lifestyle to a saprotrophic one. The fungus can colonize and decompose dead plant tissues, such as leaf litter and stem fragments, utilizing its ability to degrade plant cell wall components acquired during its endophytic phase. This transition allows the fungus to contribute to the decomposition process and nutrient cycling in the ecosystem. This example highlights the adaptability and flexibility of certain endophytic fungi to switch between lifestyles and utilize different ecological niches, depending on environmental conditions and available resources.

(b) Transition to Pathogenicity

Certain endophytic fungi, such as some species within the *Fusarium*, possess the potential to transform into plant pathogens (Brown et al. 2016). This transition to a harmful state can occur through diverse processes, including the gain of new virulence elements or a strengthening of their pre-existing ability to harm host tissues. Endophytic fungi that undergo this transition may acquire new virulence factors through horizontal gene transfer, gene duplication, or other genetic changes. These factors enable the fungi to overcome host defenses, evade or suppress the plant's immune responses, and establish pathogenic interactions. For example, they may acquire genes encoding effector proteins that manipulate host cellular processes or toxins that directly damage plant tissues. Additionally, the transition to pathogenicity may involve an enhancement of the fungi's existing ability to damage host tissues. Endophytes that initially cause minimal harm or show weak pathogenic traits may undergo genetic or epigenetic changes that lead to increased virulence. This can result in the development of disease symptoms and more severe damage to the host plant.

The transition from an endophytic lifestyle to pathogenicity is influenced by complex interactions between the fungal genetic background, host plants, and environmental factors. It represents an evolutionary process where endophytic fungi exploit their existing relationships with host plants to evolve into pathogens capable of causing disease. An example of endophytic fungi transitioning to a pathogenic lifestyle is seen in the case of the fungus *Colletotrichum*. *Colletotrichum* species are known to establish endophytic associations with various host plants. However, certain strains within this genus have evolved into devastating plant pathogens causing diseases such as anthracnose (Schulz & Boyle 2005). While numerous strains of *Colletotrichum higginsianum* manifest an endophytic lifestyle, a subset have experienced genetic alterations and gained new virulence factors, empowering them to transform into pathogens. This transformation has been observed in studies where certain strains of *C. higginsianum*, originally endophytic, caused anthracnose disease in plants like *Brassica* species when genetic modifications occurred (O'Connell et al. 2004). These pathogenic strains can overcome host defenses, colonize plant tissues extensively, and induce characteristic disease symptoms such as leaf spots and tissue necrosis.

The transition to pathogenicity in *Colletotrichum* involves genetic modifications that enhance the fungus's ability to damage host tissues and establish infection. This example highlights how certain endophytic fungi can evolve into pathogens by acquiring virulence factors or by enhancing their existing pathogenic traits.

(c) Ecological Drivers

The evolution of different fungal lifestyles is influenced by a combination of ecological pressures and genetic factors (Porras-Alfaro & Bayman 2011). For example, in the case of mycorrhizal fungi, shifts in host availability can drive the evolution of different fungal lifestyles. When certain host plant species become more abundant or dominant in an ecosystem, mycorrhizal fungi may adapt and diversify their lifestyles to colonize and form mutualistic associations with these new host species. Factors such as competition for resources can shape fungal lifestyle evolution. For instance, in the case of wood-decaying fungi, competition for limited wood resources can drive the evolution of different lifestyles. Some wood-decaying fungi may adapt to specialize in decomposing specific types of wood, while others may evolve to colonize a broader range of wood substrates, allowing them to exploit available resources and outcompete other fungi in their ecological niche. For example, fungi like *Piptoporus betulinus* have adapted to specifically decompose birch wood, while others like *Trametes versicolor* have a broader substrate range and can colonize a wide variety of wood types (Rayner & Boddy 1988, Hiscox et al. 2015). Environmental changes can also influence fungal lifestyle transitions. A well-known example is the transition of some fungi from a saprotrophic lifestyle to becoming plant pathogens under favorable environmental conditions. For instance, in the presence of high humidity and susceptible host plants, some saprotrophic fungi such as *Botrytis cinerea* can switch to a pathogenic lifestyle, causing diseases like gray mold in various crops. Genetic factors interact with ecological pressures to shape fungal lifestyle evolution. Genetic changes, such as mutations or horizontal gene transfer, can contribute to the acquisition of new traits that enable fungi to transition between lifestyles. One example is the evolution of pathogenicity in the fungus Magnaporthe oryzae, the causal agent of rice blast disease. Through genetic changes, this fungus acquired virulence factors that allow it to breach host defenses and cause disease symptoms, enabling its transition from an endophytic-like lifestyle to a destructive pathogen. By considering both ecological pressures and genetic factors, we can gain a better understanding of how different fungal lifestyles emerge and persist in response to changing environmental conditions and competitive interactions.

(d) Genetic Factors

Genetic changes, including mutations, gene duplications or losses, and horizontal gene transfer, are likely instrumental in driving these evolutionary transitions (Croll & McDonald 2012). For example, mutations can contribute to the evolution of different fungal lifestyles. In the case of the endophytic fungus *Epichloë festucae*, mutations in specific genes have been found to influence its transition from a symptomless endophyte to a fungus that induces disease symptoms in its grass host (Schardl et al. 2013). These mutations affect the production of secondary metabolites and alter the fungus's interactions with the host, enabling the transition from mutualistic endophyte to pathogenic fungus.

Gene duplications can also contribute to the evolution of different lifestyles. In the filamentous fungus *Aspergillus nidulans*, the duplication of a gene involved in the production of a secondary metabolite called sterigmatocystin resulted in the emergence of a new lifestyle variant (Lind et al. 2015, Drott et al. 2020). The duplicated gene underwent functional divergence, leading to the production of a different metabolite, penicillin, which enabled *A. nidulans* to transition to a penicillin-producing lifestyle (Böhm et al. 2013).

Gene losses can also drive evolutionary transitions in fungi. For instance, in the fungus *Batrachochytrium dendrobatidis* which causes the devastating disease chytridiomycosis in amphibians, genome analysis has revealed substantial gene losses associated with a shift to a parasitic lifestyle. The loss of genes involved in carbohydrate metabolism and cell wall synthesis is thought to have facilitated the transition from a free-living saprotrophic lifestyle to a pathogenic one (Ellison et al. 2015).

Horizontal gene transfer (HGT) can also play a role in evolutionary transitions. An example of HGT contributing to lifestyle evolution is observed in the fungus *Rhizopus microsporus*, which underwent a horizontal transfer event that introduced a carotenoid biosynthesis gene cluster from a bacterium. This transfer allowed *R. microsporus* to acquire the ability to produce carotenoids, which expanded its ecological niche and potentially facilitated its adaptation to new environments (Cissé et al. 2014).

These examples highlight how genetic changes, including mutations, gene duplications or losses, and horizontal gene transfer, can drive evolutionary transitions in fungi, leading to the development of different lifestyles and the exploration of new ecological opportunities. Understanding these transitions provides valuable insights into the evolutionary processes and ecological factors that shape fungal diversity and their roles in ecosystems. Furthermore, this knowledge has practical implications for managing plant diseases and harnessing beneficial endophytes for sustainable agricultural practices.

3.2.4. Multiple Transitions and Complex Evolutionary Trajectories

The evolutionary trajectory of endophytic fungi is complex and multifaceted, likely involving multiple transitions between different lifestyles (Rodriguez et al. 2009). Rather than being strictly categorized as endophytes, saprotrophs, or pathogens, many fungi exhibit traits of multiple lifestyles and can switch between these roles depending on the environmental context (Hacquard 2016). This flexibility may provide them with a competitive advantage in changing environments or complex ecological communities. The ability of fungi to switch between different lifestyles is facilitated by their flexible genomes, which can rapidly evolve through mechanisms such as mutation, gene duplication, and horizontal gene transfer (Croll & McDonald 2012). The latter, in particular, allows for the sharing of genetic traits between different species and can accelerate the evolution of new lifestyles.

(a) Horizontally Transferred Genes

Many fungi, including endophytes, possess genes that were acquired from other organisms through horizontal gene transfer (HGT), a phenomenon observed in a wide range of species and described extensively in scientific literature (Richards et al. 2009, Keeling & Palmer 2008). This method of non-parental gene acquisition enables organisms to adapt and evolve at a rate that exceeds the limitations of vertical inheritance (Jain et al. 1999). One key area where HGT appears to play a significant role is in nutrient uptake. Fungi, being heterotrophic organisms, are reliant on the environment for their nutritional requirements. Acquiring genes that improve nutrient absorption and metabolism can confer substantial evolutionary advantages, enabling survival in diverse environmental conditions. This concept is supported by various studies, including the work by Floudas (2021) who found that wood-decaying fungi acquired genes for lignin degradation through HGT. Immune evasion is another critical aspect of fungal biology that benefits from HGT. Fungi, especially pathogenic ones, engage in an ongoing arms race with host immune systems, and the acquisition of new evasion mechanisms can help these organisms infect a broader range of hosts or evade the host's immune responses more effectively (Frantzeskakis et al. 2020). For instance, Marcet-Houben & Gabaldón (2010) have identified multiple cases of horizontal gene transfer (HGT) between fungi and bacteria, including some that may contribute to immune evasion. An example of this is the transfer of bacterial genes encoding for effector proteins into fungal genomes, which can contribute to the fungal ability to suppress or evade plant immune responses (Khaldi et al. 2008, Marcet-Houben & Gabaldón 2010). Finally, the production of secondary metabolites, chemical compounds that are not essential for the organism's survival but often confer competitive advantages, is another area where fungi have gained benefits from HGT (Alam et al. 2021). These metabolites can serve various functions such as defense against predators, competition with other organisms, or symbiosis with hosts. The work of Slot & Rokas (2011) found that the genes involved in the biosynthesis of secondary metabolites in *Aspergillus* fungi were likely acquired via HGT from bacteria. These examples of HGT illustrate its significant role in facilitating the transition between different fungal lifestyles. By acquiring beneficial genes from other organisms, fungi can rapidly adapt to new environments or lifestyles, underscoring the pivotal role of HGT in fungal evolution (Gladieux et al. 2015, Bahram & Netherway 2022).

(b) Shared Genetic Traits

The sharing of genetic traits between endophytic and pathogenic fungi can blur the lines between these lifestyles. Both types of fungi need to overcome similar barriers to establish an interaction with the plant host, including penetrating plant tissues and dealing with the plant's immune responses. Endophytes and pathogens can share genes that enable them to achieve these feats. This includes genes coding for effector proteins that can modulate the plant's immune response, enzymes that can degrade plant cell walls, and transporters that can absorb nutrients from the plant (Schulz & Boyle 2005, German et al. 2023). However, the outcome of these interactions can differ vastly, depending on the balance of power between the plant and the fungus, and the environmental conditions. For instance, while a pathogen might cause disease by damaging plant tissues and extracting nutrients aggressively, an endophyte might achieve a more balanced relationship, living inside the plant without causing apparent harm and possibly offering benefits to the plant (Rodriguez et al. 2009, Dastogeer & Wylie 2017). The phenomenon where a fungus can switch from an endophytic to a pathogenic lifestyle under certain conditions – known as the endophyte-pathogen continuum – reflects the shared genetic traits and the dynamic nature of plant-fungus interactions (Rodriguez et al. 2009, Derafshi 2015).

The evolution of endophytic fungi involves complex transitions between different lifestyles and is facilitated by the flexible nature of fungal genomes. This complexity underscores the need for a nuanced understanding of fungal biology and ecology, taking into account the potential for lifestyle switches and the influence of environmental factors (Miyauchi et al. 2020, Drew et al. 2021, Bahram & Netherway 2022, Yang et al. 2022). It also highlights the importance of genomic research in unraveling the evolutionary history and ecological roles of these fascinating organisms. The evolution of endophytism has been shaped by multiple factors and involved numerous transitions between different lifestyles (Rodriguez et al. 2009, Naranjo-Ortiz & Gabaldón 2019). The prevalence of endophytic lifestyles across diverse fungal lineages highlights the ecological significance of endophytism and suggests that it has played a crucial role in the diversification and adaptation of fungi to various environments and hosts (Saikkonen et al. 1998, Bhunjun et al. 2023).

4. Factors Influencing the Evolution of Endophytism

The evolution of endophytism in fungi has likely been influenced by a variety of ecological factors. These factors can shape the fitness landscapes in which fungi evolve, thereby influencing the evolutionary trajectories of different lifestyles (Porras-Alfaro & Bayman 2011). Here we explore several key ecological factors that may have driven the evolution of endophytism:

4.1. Environmental Stressors

The environmental stressors are major drivers for the evolution of endophytic lifestyles. Plants living in stressful conditions are often more susceptible to disease and have a greater need for symbiotic assistance, thereby creating opportunities for the evolution of endophytic symbiosis (Rodriguez et al. 2009).

4.1.1. Drought and Temperature Extremes

Endophytic fungi can confer enhanced resilience to their host plants under conditions of drought or extreme temperatures. This mutualistic interaction provides a survival advantage to both the plant and the fungus, particularly in arid or climatically variable environments (Redman et al. 2002, Goss et al. 2017). Firstly, endophytic fungi can improve plant water use efficiency, which is especially beneficial during periods of drought. This can occur through various mechanisms, such as enhancing root hydraulic conductivity, increasing root biomass to access more water from the soil, or modifying stomatal behavior to reduce water loss through transpiration (Nisa et al. 2015, Manzur et al. 2022). In a study conducted by Xu et al. (2017), the endophytic fungus *Piriformospora indica* was found to enhance abscisic acid (ABA) levels in maize plants under drought stress. The presence of *P. indica* increased the expression of ABA biosynthesis genes in the roots of maize plants, resulting in higher ABA concentrations. This increased ABA production facilitated better water retention and improved drought tolerance in the plants. ABA can induce stomatal closure, reducing water loss, and trigger other adaptive responses in plants (Xu et al. 2002, Bharath et al. 2021). Thirdly, endophytic fungi can produce protective compounds that help plants tolerate extreme temperatures. For example, they may produce heat shock proteins, antioxidants, or other protective compounds that can mitigate the damaging effects of heat stress on plant cells (Redman et al. 2002, Lugtenberg et al. 2016, Omomowo et al. 2023). These adaptations likely evolved as a response to arid or variable climates, where the ability to withstand drought or temperature extremes would confer a significant survival advantage. This mutualistic relationship can enhance the resilience of both plants and endophytic fungi to environmental stresses, with potential implications for plant survival and productivity under climate change.

4.1.2. Nutrient Deficiency

Endophytic fungi indeed play a vital role in facilitating plant nutrient uptake and utilization, particularly in nutrient-poor environments. By doing so, they provide their host plants with a significant survival advantage and contribute to the sustainability of various ecosystems (Smith & Read 2010). One-way endophytic fungi enhance nutrient availability is through their ability to solubilize and absorb nutrients from the soil. For instance, endophytic fungi such as *Fusarium*, *Fomitopsis*, *Aspergillus*, *Alternaria*, and *Penicillium* species produce specific enzymes like phosphatases and siderophores that can break down complex organic matter or mineralize inorganic substances, thus making nutrients more readily available for plant uptake (Kasana et al. 2017, Adhikari & Pandey 2019, Turbat et al. 2020). Another strategy employed by endophytic fungi is the production of plant growth-promoting compounds. These compounds can stimulate root growth or improve the plant's nutrient assimilation efficiency. For instance, *Trichoderma* produces auxins that promote root elongation and branching, or siderophores that chelate iron and facilitate its uptake by plant roots (López-Bucio et al. 2015, Contreras-Cornejo et al. 2016). These symbiotic relationships between endophytic fungi and plants are particularly advantageous in nutrient-poor soils, where plants may struggle to acquire necessary nutrients. Over time, these beneficial interactions likely played a crucial role in driving the evolution of endophytic symbiosis in such challenging environments. This increased understanding of the beneficial roles of endophytic fungi in plant nutrient uptake and use has important implications for sustainable agriculture and ecosystem management, especially in the context of increasing nutrient scarcity and climate change.

4.1.3. High UV Radiation

Endophytic fungi can indeed contribute to the plant's resistance to high ultraviolet (UV) radiation, which can be particularly beneficial in environments with high UV exposure, such as high altitudes or latitudes (Arnold et al. 2003). One mechanism through which endophytes can provide UV protection is the production of UV-absorbing compounds, such as melanin. Melanin is a dark pigment produced by many fungi that can absorb and dissipate UV radiation, thus preventing it from causing damage to plant tissues (Bell & Wheeler 1986). Moreover, endophytic fungi can produce antioxidants that can neutralize reactive oxygen species (ROS) produced as a result of UV exposure. These ROS can cause oxidative damage to plant cells, but the antioxidants produced by endophytes can help to mitigate this damage. For example, coumarin analogue NFA from endophytic *Aspergillus fumigatus* improves drought resistance in rice as an antioxidant (Qin et al. 2019). Therefore, endophytic fungi can enhance plant resistance to high UV radiation, which can be especially beneficial in environments with high UV exposure. This could have been a driving factor in the evolution of endophytic lifestyles in such environments. The ability of endophytic fungi to enhance plant UV resistance could have implications for plant survival and productivity under climate change, which is expected to increase UV radiation levels in many parts of the world.

4.1.4. Mutual Benefits

The mutualistic relationship between endophytic fungi and their host plants indeed confers benefits to both parties involved. In providing services to their host plants – such as enhancing nutrient uptake, improving stress tolerance, or offering protection against pathogens – endophytic fungi can also indirectly secure their own survival and reproduction (Porras-Alfaro & Bayman 2011). When endophytic fungi improve the health and vitality of their host plants, they're also enhancing the environment from which they derive nutrients and in which they reproduce. This makes the symbiotic relationship a strategic advantage for their own survival. By colonizing plant tissues, they gain access to a relatively stable habitat, shielded from many of the extremes of temperature, moisture, and competition that characterize soil or surface environments (Rodriguez et al. 2009). Moreover, endophytic fungi can gain a competitive advantage over other microbial species by living inside the plant. The interior of a plant is a relatively exclusive habitat, and those fungi that have managed to colonize it face fewer competitors than they would in the soil or on the plant's surface. Thus, endophytic fungi can potentially exploit the plant's resources more efficiently and avoid competition (Gupta et al. 2020). While endophytic fungi play a vital role in promoting plant health and productivity, these mutualistic relationships also offer significant benefits for the fungi themselves.

4.1.5. Genetic and Ecological Factors

The evolution of endophytic fungal adaptations is a complex interplay of genetic changes and ecological factors.

(a) Genetic Changes

Genetic changes could involve mutations, which are random changes in DNA sequences, or horizontal gene transfer, which is the exchange of genetic material between different organisms. These changes can lead to the evolution of novel traits, including those that enhance a fungus' ability to survive within a plant or improve a plant's stress tolerance. For example, endophytic fungi might acquire genes that enable them to suppress the plant's immune response, withstand the plant's internal conditions, or produce compounds that help the plant cope with stress (Richards et al. 2009).

(b) Ecological Factors

On the other hand, ecological factors – such as environmental stressors – could create selective pressures that favor these genetic adaptations. For instance, in a drought-prone environment, plants and fungi with adaptations for drought tolerance would have a higher survival and reproduction rate, leading to the proliferation of these traits over time (Rodriguez et al. 2009). Such selection pressures could drive the evolution of endophytes towards symbiotic relationships that confer stress tolerance to the host plants.

Therefore, both genetic and ecological factors contribute to the evolution of endophytic fungal adaptations. Understanding these dynamics can shed light on how these fascinating symbiotic relationships have evolved and how they might continue to evolve in the face of environmental change. Environmental stressors are key drivers for the evolution of endophytic lifestyles, promoting the development of mutualistic symbioses that enhance plant stress tolerance. Understanding these processes can provide insights into the ecology and evolution of endophytic fungi, and can also have practical implications, such as the development of strategies to enhance crop stress tolerance in a changing climate.

4.2. Competition for Resources

The competition for resources is a significant ecological driver of endophytism. As endophytes, fungi can gain a competitive advantage by accessing the nutrient-rich, relatively competition-free niche within plant tissues (Schulz & Boyle 2005).

4.2.1. Access to Stable and Protected Environment

The plant interior indeed provides endophytic fungi with a relatively stable, protected environment that is often buffered from environmental extremes such as temperature fluctuations, UV radiation, and desiccation. This relatively predictable environment can offer significant advantages to endophytes over external environments (Redman et al. 2001). Firstly, the endophytic fungi residing within plant tissues can access a constant and readily available supply of nutrients derived from the plant's metabolic activities. This resource access is crucial for the fungi's growth and reproduction, and is often a more consistent nutrient supply than what is available in the soil, especially in nutrient-poor environments (Lebreton et al. 2021). Secondly, by inhabiting the plant's interior, endophytes are generally shielded from predation and competition, factors that frequently drive the survival and evolution of soil-dwelling microbes. The plant interior represents a niche with fewer competitors and predators, potentially allowing endophytes to proliferate more readily (Porras-Alfaro & Bayman 2011). Additionally, the plant can offer physical protection to endophytes. The robust plant structure can shield endophytes from various forms of physical damage, such as abrasion or crushing, that are common in external environments (Redman et al. 2001). The relative stability and protection offered by the plant interior, along with the constant nutrient supply, make it an attractive environment for endophytic fungi, shaping the dynamics of plant-endophyte interactions.

4.2.2. Advantage in Nutrient-Poor Environments

The endophytic lifestyle provides fungi with a significant advantage in nutrient-poor environments. Plants, as photosynthetic organisms, are capable of generating organic compounds such as sugars and amino acids from simple inorganic materials. As a result, they serve as a stable source of nutrients for endophytes, particularly in environments where nutrients are otherwise scarce or difficult to access (Naranjo-Ortiz & Gabaldón 2019). Endophytes can penetrate plant tissues and establish close contact with plant cells, enabling them to extract nutrients directly from the host. This ability allows endophytes to bypass the intense competition among soil microbes for organic material, particularly in nutrient-poor soils (Smith & Read 2010). Moreover, certain endophytes can stimulate plant growth or enhance nutrient uptake, thereby further increasing the available nutrient supply. For instance, endophytes like *Glomus intraradices, Glomus mossae* and *Trichoderma atroviride* have been reported to promote wheat plant growth and enhance nutrient uptake, particularly phosphorus, in various plant species (Colla et al. 2015). Endophytes can also benefit from the plant's ability to adapt to nutrient-poor conditions. This is seen with endophytes like *Piriformospora indica* that aid host plants in adapting to nutrient-deficient conditions (Verma et al. 2021). For example, plants can adjust their root architecture, exude organic acids to solubilize soil nutrients, or form symbiotic associations with mycorrhizal fungi to enhance nutrient uptake. By associating with plants, endophytes can indirectly benefit from these adaptations (Trivedi et al. 2020). Therefore, the endophytic lifestyle provides fungi with a unique adaptation strategy in nutrient-poor environments, ensuring a reliable nutrient supply and reducing competition with other soil microbes.

4.2.3. Co-evolution and Symbiotic Relationships

Co-evolution and symbiotic relationships are fascinating phenomena that occur in various ecosystems, including the mutualistic association between plants and fungi. This close association between plants and fungi can lead to co-evolutionary processes, wherein both organisms adapt and evolve in response to each other's presence. The concept of co-evolution was extensively discussed by van der Heijden et al. (2008). In this mutually beneficial relationship, the fungi obtain a stable source of nutrients and a protected habitat by colonizing the roots of plants, forming structures known as mycorrhizae. In return, the fungi can provide several advantages to the plants they associate with. The benefits offered by the fungi can vary and depend on the specific symbiotic relationship. One crucial benefit is the enhancement of nutrient uptake by the plant. Fungi possess an extensive network of fine filaments called hyphae, which can efficiently explore the soil and acquire nutrients that may be inaccessible to the plant's root system alone. The mycorrhizal association facilitates the transfer of these nutrients from the fungi to the plant, thus improving its overall nutrient acquisition (Rodriguez et al. 2009).

Furthermore, certain types of fungi within the mycorrhizal symbiosis can produce growth-promoting hormones, such as auxins and cytokinins. These hormones can stimulate plant growth, including root development, which, in turn, can enhance nutrient absorption and overall plant productivity. The secretion of growth-promoting hormones by the fungi represents another way in which they contribute to the plant's well-being (Rodriguez et al. 2009). In addition to nutrient acquisition and growth promotion, mycorrhizal fungi can also provide protection to their host plants against various pathogens and pests. The symbiotic relationship can trigger the plant's defense mechanisms, leading to an enhanced resistance to harmful microorganisms or insects. The fungi can also directly compete with pathogens for nutrients and space, effectively reducing their impact on the plant's health. These protective effects are particularly relevant in agricultural systems, where the use of mycorrhizal fungi has been explored as a sustainable alternative to chemical pesticides (Rodriguez et al. 2009). The co-evolution of plants and fungi in symbiotic relationships results in mutual benefits. The plants receive improved nutrient uptake, growth promotion, and protection against pathogens and pests from the fungi, while the fungi gain a stable source of nutrients and a protected habitat.

This intricate interplay between plants and fungi highlights the complexity and importance of symbiotic relationships in shaping ecological communities.

4.2.4. Genetic Adaptations

The transition to an endophytic lifestyle is believed to involve a series of genetic adaptations that allow the fungi to successfully inhabit plant tissues. For an endophyte, penetrating plant tissues, extracting nutrients, suppressing or evading the plant's immune response, and tolerating the plant's internal conditions are vital survival tactics, and these skills may be supported by specific genetic adaptations (Porras-Alfaro & Bayman 2011). For example, certain endophytes possess genes that code for enzymes capable of degrading plant cell walls, allowing the fungi to penetrate plant tissues (Verena et al. 2011). Other genetic adaptations might involve mechanisms for extracting and metabolizing nutrients from plant tissues, or for tolerating the plant's internal conditions, such as variations in pH, oxygen levels, or the presence of antimicrobial compounds (Hacquard et al. 2016).

Furthermore, endophytes must be able to suppress or evade the plant's immune response to establish and maintain a successful colonization. For example, endophytes like *Fusarium oxysporum* achieve this by producing effector proteins that interfere with the plant's immune signaling pathways (Michielse & Rep 2009), while others like Epichloë festucae may disguise themselves or hide within plant cells to avoid detection (Schulz & Boyle 2005). In addition, horizontal gene transfer (HGT) can also contribute to these adaptations. HGT allows for the rapid acquisition of beneficial traits from other microbes, potentially accelerating the adaptation of endophytes to their host plants or enabling them to cope with new challenges or environmental changes (Richards et al. 2009). Hence, understanding the genetic adaptations associated with the endophytic lifestyle can provide important insights into the mechanisms of plant-endophyte interactions and help identify potential strategies for harnessing endophytes in sustainable agriculture and ecosystem management. Competition for resources is a key driver for the evolution of endophytic lifestyles. By colonizing the plant interior, endophytes can access a stable source of nutrients and avoid the intense competition in the external environment. Understanding these processes can provide insights into the ecological roles and evolutionary trajectories of endophytic fungi.

4.3. Host Plant Diversity

The diversity of host plants plays a significant role in shaping the evolution and specialization of endophytic fungi. As endophytes interact with their hosts, a myriad of factors come into play, influencing the direction of evolutionary pathways (Saikkonen et al. 1998).

4.3.1. Host Susceptibility to Colonization

Different plant species indeed vary considerably in their susceptibility to fungal colonization due to the diversity in their physical and chemical defenses. The interaction between a plant and an endophyte is a dynamic process, shaped by both the plant's defense mechanisms and the endophyte's adaptive strategies (Slippers & Wingfield 2007). Physically, plant defenses include elements such as the thickness and composition of their cell walls. A thicker cell wall can make it harder for endophytes to penetrate and colonize plant tissues (Underwood 2012). Also, the pattern and density of stomata and trichomes on leaves can influence the ability of fungi to adhere to and invade the plant.

Chemically, plants produce a variety of antimicrobial compounds that can inhibit the growth and development of fungi. These include phytoalexins, pathogenesis-related proteins, and other secondary metabolites. Certain plants, like *Nicotiana attenuata*, are known to produce specific volatile organic compounds, like cis-α-bergamotene, that can deter endophytes (Meldau et al. 2011). The plant's immune system also plays a crucial role in its susceptibility to fungal colonization. Some plants, such as *Arabidopsis thaliana*, have robust immune systems capable of recognizing and effectively responding to fungal invaders through mechanisms such as systemic acquired resistance and induced systemic resistance (Jones & Dangl 2006). The differential susceptibility of plants to fungal colonization can lead to the evolution of endophytes that are specialized to overcome the defenses of specific host plants. These endophytes may evolve mechanisms to degrade or bypass cell walls, detoxify antifungal compounds, or suppress plant immune responses (Hardoim et al. 2015). Understanding the factors that determine a plant's susceptibility to fungal colonization can inform strategies to manage plant health and disease, such as breeding for enhanced disease resistance or manipulating the plant microbiome for improved health and productivity.

4.3.2. Diversity in Resources Provided by Host

The diversity in resources offered by host plants can significantly influence the community structure of endophytic fungi and drive the evolution of specialized endophytic relationships (Redman et al. 2001). The availability and type of nutrients within plant tissues can greatly affect the composition and diversity of endophytic communities. Different plant species, and even different tissues within the same plant, can vary considerably in their nutrient content, influencing which endophytic fungi can thrive there. For example, high sugar concentrations in phloem tissues may favor endophytes capable of metabolizing these compounds, while endophytes in nitrogen-rich tissues such as leaves might evolve mechanisms to efficiently utilize these nutrients (Schulz & Boyle 2005).

The structure and composition of plant tissues can also influence endophyte community dynamics. For instance, certain endophytes like *Xylaria* species are better equipped to colonize the dense, fibrous tissues of woody plants (Fisher & Petrini 1992), while others like *Colletotrichum* species may prefer the softer tissues of herbaceous plants (Arnold et al. 2003, Rodriguez et al. 2009). The spatial structure within plant tissues, such as the arrangement and accessibility of plant cells, can similarly affect endophyte colonization and distribution within the plant. Moreover, the environmental conditions within plant tissues, such as temperature, pH, and oxygen levels, can also play a role in shaping the endophytic community. Endophytes must be able to tolerate and adapt to these microenvironmental conditions in order to successfully colonize plant tissues (Porras-Alfaro & Bayman 2011).

These different factors can lead to the evolution of endophytes that are specialized to exploit the unique resources and conditions provided by their host plants. Understanding these endophyte-host dynamics can be crucial for developing strategies to harness endophytes for improving plant health and productivity.

4.3.3. Co-evolution and Host Specificity

The intricate relationship between plants and their endophytic fungi often leads to co-evolution and host specificity, where certain endophytes are uniquely adapted to colonize particular host plants. This phenomenon is frequently observed in mutualistic relationships, as both parties have evolved mechanisms to mutually benefit each other (van der Heijden et al. 2015). Co-evolution in these relationships may manifest as the development of unique structures, behaviors, or physiological adaptations that enhance the symbiotic relationship. For example, in mycorrhizal associations, the plant provides the fungus with carbohydrates, while the fungus improves the plant's nutrient uptake by increasing the root surface area for nutrient absorption (Smith & Read 2010).

Moreover, the endophyte may help the plant cope with environmental stresses, such as drought, salinity, or extreme temperatures, by altering plant physiology or gene expression (Rodriguez et al. 2008). Endophytes can also bolster the plant's defense against pathogens or herbivores, either by producing antimicrobial compounds or by priming the plant's immune response (Bollmann-Giolai et al. 2022). In return, the plant offers the endophyte a sheltered habitat and a consistent supply of nutrients, thus enabling the endophyte to complete its lifecycle. For example, plants like *Allium sativum* (garlic) are known to produce specific compounds, such as alliin, that stimulate the growth of their symbiotic fungi, *Penicillium allii*, or selectively suppress non-symbiotic species (Zamioudis & Pieterse 2012, Hayat et al. 2016).

This co-evolutionary process can result in a high degree of host specificity, where certain endophytes are found only in specific plant species or within certain tissues of a plant. Understanding these specialized relationships can offer crucial insights into the dynamics of plant-endophyte interactions and their potential applications in agriculture and ecosystem management.

4.3.4. Influence on Community Structure

Host plant diversity plays a significant role in shaping the structure of endophytic fungal communities. The variety of different plant species and their individual characteristics can foster diverse communities of endophytic fungi, as each plant species may host a unique assortment of endophytes (Arnold et al. 2007). Different plant species may vary in terms of their physical structures, chemical compositions, defense mechanisms, and environmental conditions, all of which can influence the types of endophytes that they can host. Furthermore, different plant tissues (e.g., roots, leaves, stems) can also host distinct endophytic communities, adding another layer of complexity to these interactions (Hardoim et al. 2015).

Changes in plant diversity, such as those caused by habitat disturbance or climate change, can thus lead to shifts in endophyte diversity. These shifts can have significant consequences for ecosystem processes. For instance, endophytes play key roles in nutrient cycling by decomposing organic matter and transforming nutrients into forms that are accessible to plants. Changes in endophyte diversity can, therefore, affect nutrient availability and plant productivity (van der Heijden et al. 2008). Moreover, endophytes can also impact plant communities by altering plant growth, survival, and competitive interactions. For example, endophytes like *Neotyphodium coenophialum* can enhance plant resistance to pathogens or environmental stressors (Hunt & Newman 2005), while other endophytes such as *Metarhizium robertsii* can influence plant-insect interactions (Behie & Bidochka 2014a). Similarly, the presence of endophytic fungi has been found to influence plant-pollinator relationships (Vannette & Fukami 2016). These effects can ultimately shape plant community structure and dynamics, demonstrating the far-reaching implications of plant-endophyte interactions for ecosystem health and resilience.

The diversity of host plants can influence the evolution of endophytic fungi in various ways, leading to the evolution of specialized endophytic relationships and shaping the structure of endophytic fungal communities. This highlights the importance of considering both the fungal and plant perspectives when studying endophytic symbioses.

4.4. Co-evolution with Other Organisms

Interactions with other organisms play a crucial role in the evolution of endophytic fungi. These interactions create a complex web of ecological relationships that exert strong selective pressures on endophytic fungi, influencing their evolutionary trajectories.

4.4.1. Herbivores and Plant Pathogens

Herbivores and plant pathogens indeed exert significant selective pressures on endophytic fungi, shaping their evolution. By creating threats to the plant host, these pressures stimulate the evolution of protective traits in endophytes. Endophytes can deter herbivores and pathogens through various strategies. For instance, they can produce toxic or deterrent compounds that ward off herbivores or inhibit pathogen growth. A notable example is the production of alkaloids by the endophytic fungi of the genus *Epichloë* in grass species. These alkaloids deter grazing by herbivores and confer a survival advantage to the host plant in regions with high herbivore presence (Clay 1988). In addition to producing defensive compounds, endophytes can also enhance the host plant's defenses. For example, some endophytes can enhance the plant's production of defensive compounds or bolster the plant's immune responses. The endophyte *Piriformospora indica*, for instance, has been found to boost the immunity of its host plant *Arabidopsis thaliana*, making it more resistant to pathogen infection (Jacobs et al. 2011). Interestingly, certain endophytes may even adopt a more aggressive strategy, directly parasitizing invaders. This phenomenon is seen with endophytic fungi such as *Trichoderma* species, that can parasitize plant pathogens, inhibiting their growth and limiting their damage to the host plant (Harman et al. 2004, Rodriguez & Redman 2008). These various defensive strategies, driven by the pressure exerted by herbivores and plant pathogens, highlight the pivotal role that these biotic factors play in shaping the evolution of endophytic fungi. These pressures can favor endophytes that protect their host plants, thus ensuring the preservation of their own habitat.

4.4.2. Interactions with Other Endophytes

Interactions between endophytic fungi within the host plant environment indeed play a substantial role in shaping the endophytic community's structure and function. These interactions, whether they be competitive or cooperative, have substantial implications for the evolution and ecological dynamics of these communities. Competition among endophytes arises due to the finite resources within a plant. Limited nutrient availability can lead to competition, driving the evolution of traits that enhance resource acquisition or inhibit rival endophytes. For instance, endophytes like *Streptomyces* species have been observed to produce antimicrobial compounds that inhibit the growth of other endophytes, thereby reducing competition for resources (Saikkonen et al. 2004, Seipke et al. 2012). On the other hand, cooperation or synergy among endophytes can also occur. Endophytic fungi, organisms living inside plants, present a fascinating diversity of interactions with their hosts, often providing significant benefits. For instance, *Cladosporium cladosporioides* and *Penicillium citrinum*, isolated from the medicinal plant Hypericum perforatum, when co-cultured, produce a unique compound not seen when they were grown individually, demonstrating a complementary relationship in their metabolic processes (Gao et al. 2010). Similarly, different *Epichloë* species, endophytes found in many grass species, produce varied alkaloids that offer a broad spectrum of protection against herbivores, benefiting plants hosting multiple *Epichloë* species (Schardl et al. 2004). Another example is the combination of *Piriformospora indica* and *Phoma* sp., which upon joint colonization reduces disease symptoms more significantly than when present independently (Waller et al. 2005). These examples underline the extensive potential and complexity of endophytic fungi complementing each other's capabilities and jointly defending their host plants. The presence of antagonistic and synergistic interactions can lead to the evolution of complex endophytic communities within a single host plant. This complexity can have significant implications for the health and resilience of the plant host, underlining the importance of understanding these interactions.

4.4.3. Interactions with Soil Microbes

Interactions with soil microbes indeed play an essential role in shaping the evolution of endophytic lifestyles. The soil environment, rich with microbial life, presents both opportunities and challenges for endophytes, and these interactions can drive the evolution of key traits in these fungi. Soil microbes, such as bacteria and other fungi, may compete with endophytes for resources in the rhizosphere, the region of soil directly influenced by root secretions and associated soil microorganisms. The competition can be intense, driving the evolution of traits that enhance nutrient acquisition or inhibit rival microorganisms. For instance, endophytes like *Pseudomonas fluorescens* can produce antifungal or antibacterial compounds to suppress the growth of competing microbes (Dudeja et al. 2012, Weller 2007). On the other hand, certain soil microbes such as mycorrhizal fungi can facilitate the colonization of plants by endophytic fungi (Selosse et al. 2006). These microbes could suppress the plant's immune response, creating a more conducive environment for endophytic colonization. Other microbes might create physical entry points in plant tissues, further easing the way for endophytes. For instance, certain plant pathogenic fungi can cause wounds in plant tissues, which can then be exploited by opportunistic endophytic fungi for entry (Petrini 1991).

In addition, soil microbes and endophytes might also engage in cooperative or synergistic interactions. Certain bacterial species in the rhizosphere can promote fungal growth or assist in nutrient uptake, thereby favoring endophytic colonization. In conclusion, interactions with soil microbes can shape the evolution of endophytic fungi in various ways. These interactions can drive the evolution of traits related to root colonization, competition, or cooperation, thereby influencing the composition and activity of the endophytic community. The interactions of endophytic fungi with other organisms play a significant role in shaping their evolution. These interactions create a complex web of ecological relationships exerting strong selective pressures, leading to the evolution of a diverse range of traits and lifestyles. Understanding these processes can provide valuable insights into the ecological roles and evolutionary trajectories of endophytic fungi.

4.5. Habitat and Geographic Isolation

Habitat characteristics and geographical isolation play pivotal roles in the evolution and distribution of endophytic fungi. Various factors related to climate, geography, and habitat-specific conditions can influence these dynamics.

4.5.1 Climate

Climate does play a significant role in shaping the composition and diversity of endophytic fungi. This is seen most markedly in comparisons between different biomes, such as tropical versus temperate regions. In tropical regions, which are characterized by warm temperatures and high humidity, a rich diversity of endophytes can be found. The conditions in these regions not only provide an ideal environment for fungal growth but also support a wide range of host plants, thus creating a broad spectrum of niches for endophytes to occupy. An illustrative example comes from a study in Costa Rica, where the endophytic diversity in tropical trees was found to be extremely high, hosting hundreds of unique endophytic species (Del Olmo-Ruiz & Arnold 2014). Conversely, temperate regions typically host a smaller diversity of endophytes. This is not only due to the less diverse range of potential host plants but also due to the more challenging growth conditions. However, certain endophytes can be particularly adapted to these environments. For instance, a study in temperate grasslands found a unique assemblage of endophytic fungi that have evolved to withstand the colder temperatures and reduced light conditions characteristic of these regions (Saunders et al. 2010). Specific climatic conditions can indeed lead to the evolution of climate-specific endophytic traits. These endophytes are then well-adapted to their local environments and may play essential roles in helping their host plants cope with these same conditions. An example is seen in *Thermomyces* endophytes in desert plants, which have been shown to provide their hosts e.g., cucumber with enhanced drought tolerance, a crucial trait in arid climates (Rodriguez et al. 2008, Ali et al. 2018). Climate is a major factor in shaping the distribution, diversity, and adaptations of endophytic fungi, with profound implications for plant health and ecosystem functioning.

4.5.2. Geographical Isolation

Geographical isolation plays a significant role in shaping the genetic diversity and evolution of endophytic fungi. The concept of geographical isolation ties back to one of the basic principles of evolutionary biology – when populations of organisms are physically separated for long periods, they can diverge over time due to genetic drift and local adaptation. This divergence can result in the evolution of distinct lineages, each uniquely adapted to their specific environment. This principle can be readily observed in the world of endophytic fungi. For instance, on isolated islands, the fungal communities can evolve unique traits to adapt to the local conditions. The Hawaiian Islands, for example, are home to a variety of plant species that harbor unique assemblages of endophytic fungi, showing a high degree of endemism (Arnold & Herre 2003). The isolation of these islands has created unique ecological niches that have likely driven the evolution of these distinct endophytic communities. Similarly, mountain ranges can act as barriers to gene flow, leading to the development of distinct fungal lineages. An example can be seen in the Andes, where different elevational zones host distinct endophytic communities. These fungi have likely evolved to cope with the specific environmental conditions at different elevations, such as changes in temperature, humidity, and UV radiation (Gazis & Chaverri 2010). Geographical isolation plays a crucial role in shaping the diversity and evolution of endophytic fungi. Over time, isolated populations can evolve distinct lineages, each uniquely adapted to their specific environment.

4.5.3. Habitat-Specific Conditions

Habitat-specific conditions indeed play a substantial role in the evolution of endophytic fungi. These conditions can encompass a wide range of factors, from soil type and nutrient availability to the presence of specific plant species or other organisms, each creating a unique environmental niche with its own set of challenges and opportunities. In nutrient-poor soils, endophytes might evolve traits that enhance nutrient uptake to support their growth and survival. An example of this is seen with the endophyte *Piriformospora indica*, which can improve the phosphorus uptake in its host plant, especially in phosphorus-deficient soils (Yadav et al. 2010). Similarly, endophytes found in habitats with a high prevalence of pathogens might evolve enhanced defensive traits. As an instance, certain endophytic fungi, such as *Pestalotiopsis microspora*, generate bioactive substances that can ward off pathogens, thereby offering a protective benefit to their host plants. For instance, these fungi produce taxol, a potent antifungal compound that aids in the plant's defense against fungal pathogens (Strobel et al. 1996). In the tropical rainforest tree *Theobroma cacao*, the source of cocoa beans, certain endophytic fungi produce antifungal compounds that help protect the plant against the devastating pathogen *Phytophthora* spp., which causes a disease known as "black pod" (Arnold et al. 2003). The interplay of various habitat-specific conditions can shape the ecological niches available for endophytes, driving the evolution of a myriad of adaptations tailored to these unique environments. Understanding these complex interactions is key to appreciating the full spectrum of endophyte diversity and function.

4.5.4. Species Interactions

Geographic variation in species interactions indeed plays a pivotal role in shaping the diversity and evolution of endophytic fungi. Species interactions create complex ecological networks that can exert significant selective pressures, leading to the evolution of specialized traits in endophytic fungi. For instance, the presence or absence of certain herbivores or pathogens in a specific geographic location can create unique selection pressures. Endophytes that produce compounds deterring herbivores or inhibiting pathogen growth may have a survival advantage in regions where such threats are prevalent. An example of this interaction is seen in the grass species *Festuca arundinacea*, where endophytes produce alkaloids that deter herbivores, providing a protective benefit to the plant in environments with high herbivory pressure (Clay 1988). Furthermore, the local community of plant species can influence the diversity and evolution of endophytes. Different plants can host different endophytic communities and provide a diverse array of resources or challenges for endophytic colonization. For instance, in a mixed hardwood forest in the eastern United States, endophytic communities differed substantially between tree species, suggesting that host plant identity plays a significant role in shaping endophytic community composition (Higgins et al. 2007). Geographic variation in species interactions, whether they are between plants, endophytes, herbivores, or pathogens, creates a mosaic of selective pressures that can drive the evolution of endophytic fungi. Habitat characteristics and geographical isolation can significantly influence the evolution and distribution of endophytic fungi. This underscores the importance of considering environmental and geographic factors when studying the ecology and evolution of endophytic symbioses. The evolution of endophytism in fungi is likely to have been driven by a combination of these ecological factors. Understanding these factors can provide valuable insights into the evolutionary history of endophytism and the diverse roles that endophytes play in different ecosystems.

4.6. Host Plant Factors

In addition to the ecological factors previously discussed, certain characteristics of host plants can significantly influence the evolution and diversification of endophytic fungi. Here, we delve into key host-related factors that may shape the presence and functional roles of endophytes.

4.6.1. Plant Susceptibility

Variation in plant susceptibility to endophytic fungi significantly influences their lifestyle, ecological role, and evolution. This variation creates diverse ecological niches, potentially driving the evolution of host-specific adaptations.

(a) Physical and Chemical Defenses

Different plants indeed employ a diverse array of physical and chemical defenses to counteract fungal colonization. One way they achieve this is through physical barriers, like thickened cell walls or robust cuticles that deter fungal penetration. An excellent example is the outer cuticle of citrus plants, which has been reported to inhibit the penetration of various fungal pathogens, including the fungus *Penicillium digitatum* and *P. italicum* (Papoutsis et al. 2019). Chemical defenses are also a significant part of a plant's anti-fungal arsenal. They include a variety of antimicrobial compounds that can inhibit fungal growth, as well as signaling molecules that trigger plant immune responses. For instance, in grapevines, the plant produces resveratrol, a chemical compound known for its antifungal properties, particularly against *Botrytis cinerea*, a widespread fungal pathogen in vineyards (Jeandet et al. 2002, De Bona et al. 2019). Interestingly, these defenses do not just act as protective mechanisms, but they also play a role in shaping the endophytic community. Endophytes that can overcome or evade these defenses tend to be favored, which drives the evolution of host-specific adaptations. A compelling example is the endophytic fungus *Epichloë festucae*, which colonizes perennial ryegrass (Tanaka et al. 2006). This endophyte has evolved to produce the same alkaloids as its host, thereby evading the host's chemical defenses and establishing a mutually beneficial relationship (Saunders et al. 2010). Plants use physical and chemical defenses to regulate fungal colonization, leading to a dynamic interplay that shapes the diversity and adaptability of the endophyte community.

(b) Promotion of Endophyte Colonization

Plants indeed have evolved a variety of strategies to promote the colonization of certain beneficial endophytes. These strategies not only aid the plant in forming advantageous relationships but also influence the evolution of host-specific endophytes. One such strategy is the production of specific root exudates that attract beneficial endophytes. Root exudates are a mixture of organic acids, sugars, amino acids, and secondary metabolites secreted by plant roots into the surrounding soil. These exudates can selectively attract and stimulate the growth of beneficial endophytes, while deterring pathogenic microbes. For example, a study on *Medicago truncatula*, a model legume plant, showed that specific root exudates could selectively attract the beneficial endophyte *Glomus intraradices* (Bécard et al. 1992). Similarly, plants can suppress immune responses in certain tissues, allowing beneficial endophytes to establish themselves. This immune suppression is tightly regulated to avoid infection by harmful pathogens. An example can be seen in the relationship between *Arabidopsis thaliana* and the endophytic fungus *Piriformospora indica*. *Arabidopsis thaliana* allows *P. indica* to colonize its roots by suppressing immune responses in the root cortex, resulting in a mutually beneficial association (Jacobs et al. 2011). Over time, these plant strategies can drive the evolution of host-specific endophytes that are finely tuned to these signals and opportunities, fostering relationships that benefit both parties.

(c) Host-Specific Endophytes

The selective pressures exerted by host plants can drive the evolution of endophytes that are specialized to colonize specific plant species or genotypes. This specificity manifests in multiple ways, which underpins the complex and multifaceted nature of endophyte-host interactions. Firstly, specificity can be seen in endophytes exhibiting a preference for certain host species or genotypes. Some endophytes have evolved to colonize a narrow range of host species, or even specific genotypes within a species. For example, the endophytic fungus *Neotyphodium coenophialum* has a tight symbiotic relationship with tall fescue (*Festuca arundinacea*), and is rarely found in other plant species (Schardl et al. 1997). Secondly, specificity can arise from endophytes evolving the ability to overcome specific host defenses. The endophyte *Epichloë festucae*, as mentioned previously, has evolved to produce the same alkaloids as its host, perennial ryegrass (*Lolium perenne*), thereby overcoming the host's chemical defenses (Saunders et al. 2010). Lastly, specificity can be driven by endophytes relying on specific host signals or resources for colonization. This phenomenon is well-demonstrated in the interaction between the mycorrhizal fungus *Glomus intraradices* and *Medicago truncatula*, where specific root exudates from the host plant guide the colonization by the endophyte

(Bécard et al. 1992). In essence, the dynamic and selective pressures in the endophyte-host relationship led to the evolution of host-specific endophytes, showcasing the complexity and adaptability of these interactions.

(d) Intraspecific Variation

Intraspecific variation, or variation within a single plant species, indeed plays a crucial role in shaping the endophytic community. Different genotypes within the same species can exhibit significant variation in aspects such as their defenses, their signals, or the resources they offer, and this can lead to differential susceptibility to different endophytes. An example of this can be found in the relationship between the fungal endophyte *Epichloë festucae* and its host, perennial ryegrass (*Lolium perenne*) (Ma et al. 2015). Different ryegrass genotypes have been found to harbor distinct strains of *E. festucae*, showing that even within a single plant species, different genotypes can host different endophyte strains (Liu et al. 2017). Another example can be seen in maize (*Zea mays*). Here, intraspecific variation has been observed to influence the diversity of endophytic fungi. Different maize genotypes have been found to host different assemblages of endophytic fungi, showing that genotype plays a significant role in shaping the endophytic community (Johnston-Monje & Raizada 2011). This intraspecific variation creates a broad range of ecological niches for endophytes, further driving the diversification of the endophyte community and leading to the evolution of genotype-specific endophytes. This complexity underscores the profound influence that host plants exert on their endophytic partners, and highlights the importance of considering intraspecific variation when studying endophyte-host interactions. Variation in plant susceptibility to endophyte colonization, both among and within species, significantly influences the evolution of endophytic fungi. Understanding these dynamics provides valuable insights into the ecology and evolution of endophytic symbioses.

4.6.2. Plant Tissue Types

The type of plant tissue colonized by endophytic fungi significantly influences their lifestyle, ecological role, and evolution. Different plant tissues present diverse ecological niches with unique resources, challenges, and selective pressures.

(a) Root-Colonizing Endophytes

Root-colonizing endophytes play a pivotal role in the health and survival of plants, particularly in nutrient-deficient or harsh environments. Their interactions with plants often confer benefits such as enhanced nutrient acquisition and exchange, leading to improved plant growth and resilience. A key mechanism through which these endophytes assist in nutrient acquisition is by accessing and solubilizing soil nutrients that are otherwise unavailable or inaccessible to the plant. They can produce specific enzymes or secrete organic acids that solubilize nutrients such as phosphorus, making them available for the plant (Richardson et al. 2009, Behie & Bidochka 2014b). Further, many root-colonizing endophytes form symbiotic associations with the plant's root cells, known as mycorrhizae. In these associations, the fungi colonize the host plant's root tissues, increasing the surface area for nutrient absorption. This relationship also involves a mutual exchange of resources: the plant provides the fungi with carbohydrates (sources of carbon), and in return, the fungi supply the plant with essential nutrients like nitrogen and phosphorus from the soil (Smith & Read 2010, Chang et al. 2017, Genre et al. 2020). Mycorrhizal fungi are particularly noteworthy for their ability to improve the host plant's water and nutrient uptake, enhance resistance to soil-borne diseases, and increase tolerance to environmental stresses such as drought and heavy metals (Bonfante & Genre 2010, Nanjundappa et al. 2019). Understanding the interactions between root-colonizing endophytes and host plants can have significant implications for sustainable agriculture, especially in the context of climate change and decreasing soil fertility. This knowledge can guide the development of strategies to exploit beneficial plant-microbe interactions to enhance crop productivity and resilience.

(b) Stem and Leaf-Colonizing Endophytes

Endophytes that inhabit the stems and leaves of host plants are exposed to a unique set of environmental challenges, ranging from extreme light levels and ultraviolet (UV) radiation to desiccation. Additionally, these endophytes also need to participate in the defense against herbivores and pathogens. Consequently, such ecological pressures can shape the evolution of different adaptive mechanisms in these endophytes, including the development of UV damage protection, water retention capacities, and the production of deterrent or toxic compounds (Rodrigues-Heerklotz et al. 2001, Rodriguez et al. 2009, Sarkar et al. 2021). Intense light levels and UV radiation pose significant challenges to these endophytes. As a response, they have evolved mechanisms to protect against UV damage. For instance, endophytes can produce UV-absorbing secondary metabolites to shield themselves and their host plants. This UV-protective role of endophytes has been well documented in the literature. For example, Arnold et al. (2007) demonstrated the presence of UV-absorbing compounds in endophytic fungi isolated from high-altitude tropical plants.

Another environmental pressure faced by stem and leaf-colonizing endophytes is desiccation or water stress. The development of water retention mechanisms becomes crucial under these circumstances. Studies have reported that endophytes can enhance plant tolerance to drought stress. For instance, Khan et al. (2011) reported that a fungal endophyte (*Penicillium funiculosum*) improved the water use efficiency and growth of drought-stressed soya bean *Glycine max* plants. Furthermore, endophytes in stems and leaves play a pivotal role in defending their host plants against herbivores and pathogens. They can produce a variety of deterrent or toxic compounds, often as secondary metabolites, that deter herbivores or kill pathogens. Rodriguez et al. (2009), the same study you referenced, shed light on the defensive role of endophytes in host plants by discussing the production of alkaloids, a kind of toxic compound that can deter herbivores and thwart pathogens. The unique ecological pressures faced by stem and leaf-colonizing endophytes have driven the evolution of adaptive mechanisms, including UV damage protection, water retention, and production of deterrent or toxic compounds. This not only enables their survival in challenging environments but also provides a protective role to their host plants.

(c) Seed-Colonizing Endophytes

Seed-colonizing endophytes constitute a unique group of microbes with significant implications for plant health, development, and survival across generations. For instance, fungi like *Penicillium chrysogenum*, *Phoma* sp., and *Trichoderma koningii*, which are found in *Opuntia* spp., contribute to ending seed dormancy and fostering germination, as reported by Delgado-Sánchez et al. (2011, 2013). Similarly, certain endophytic fungi present in seeds from the *Ascomycota* and *Pleosporales* groups have been observed to encourage growth and germination in *Phragmites australis*, as documented by Ernst et al. (2003). Seed-colonizing endophytes may evolve several mechanisms to enhance the success of their host plants. For instance, they can promote seed germination by producing plant growth-promoting hormones or by mitigating the impact of environmental stressors on the germination process (Fahad et al. 2015). In the early stages of plant development, these endophytes can support seedling growth by enhancing nutrient uptake, increasing tolerance to environmental stresses, or stimulating the plant’s immune system to ward off potential pathogens (Johnston-Monje & Raizada 2011).

Moreover, seed-colonizing endophytes can offer protection to the seeds against biotic threats, such as pathogens and predators. They can produce a range of bioactive compounds that deter pathogenic microbes or inhibit their growth. Certain endophytes, like the fungus *Epichloë festucae*, can also deter herbivores by altering the plant’s chemistry, thereby reducing the chances of seed predation (Clay & Schardl 2002). *Trichoderma hamatum* isolate DIS 219b, offers multiple layers of protection to their host plants like promotes growth and delays the onset of the drought response in *Theobroma cacao* (Bae et al. 2009). Understanding the role of seed-colonizing endophytes in plant health and survival is of crucial importance, especially in the context of crop production and conservation efforts. They may offer an avenue for enhancing seed germination, seedling growth, and disease resistance, thus promoting sustainable agricultural practices.

(d) Tissue-Specific Adaptations

Correct, many endophytes demonstrate remarkable adaptability in their colonization patterns, displaying the ability to inhabit various plant tissues, such as roots, stems, leaves, and seeds. This adaptability allows them to take advantage of the resources available in different plant tissues and to negotiate various ecological pressures within their host plants (Hardoim et al. 2015). For instance, certain endophytes can colonize the plant's root system where they assist in nutrient acquisition, while the same endophytes might also be found in the aerial parts of the plant, where they could have roles in pathogen defense or stress mitigation (Rodriguez et al. 2009). This broad ecological competence indicates the evolution of complex or flexible lifestyles that enable endophytes to thrive in a wide range of plant tissues and environmental conditions.

To successfully colonize diverse plant tissues, these endophytes may need to overcome distinct physical and chemical barriers present in different plant parts. For example, to colonize the root tissues, endophytes must navigate the root exudate environment, negotiate root physical barriers, and interact with the existing microbiota (Phillips 2017, Kaiser et al. 2023). Meanwhile, colonization of leaf tissues would require the ability to withstand exposure to sunlight and other climatic variables while navigating the leaf surface and internal structures (Redman et al. 2001). Understanding the tissue-specific adaptations of endophytes can provide valuable insights into their diverse roles in plant health and disease. This knowledge could guide the application of endophytes in sustainable agricultural practices, such as using beneficial endophytes as biocontrol agents or biofertilizers to improve crop health and productivity. The tissue-specific context plays a significant role in shaping the lifestyle and evolution of endophytic fungi. Thus, understanding these interactions can provide valuable insights into the diversity and ecological roles of endophytes within the plant.

4.6.3. Plant Developmental Stage

The developmental stage of a host plant plays a critical role in influencing the presence, activity, and evolution of endophytic fungi. Different stages of plant growth and development can present unique opportunities and challenges for endophytic colonization, resulting in dynamic changes in the endophytic community over time.

(a) Young, Rapidly Growing Tissues

Young, rapidly growing plant tissues often have less developed physical defenses, making them more susceptible to endophytic colonization. These tissues are also typically nutrient-rich, providing an attractive niche for endophytes (Rodriguez et al. 2009, Porras-Alfaro & Bayman 2011). The developmental stage of a plant significantly impacts the presence and activity of endophytic fungi. Specifically, young, rapidly growing tissues, with their underdeveloped physical defenses, tend to be more susceptible to endophytic colonization. These tissues, rich in nutrients such as sugars, amino acids, and minerals, provide an enticing habitat for endophytes.

Endophytic fungi, while seizing the opportunity to inhabit such nutrient-rich spaces, can also contribute positively to their host plant's health during this stage. They are known to enhance the host's tolerance to environmental stressors and assist in nutrient absorption, forming a symbiotic relationship where the fungi also receive a secure, nutrient-abundant environment in return. Research on endophytic fungi in wheat (*Triticum aestivum*) found that the community composition of the fungi significantly changed as the plant matured, from seedling to tasseling stage. The endophytes present in the early growth stages were predominantly involved in promoting growth and enhancing stress tolerance (Manjunatha et al. 2022).

The relationship dynamics between endophytic fungi and their host plant can vary greatly, depending on the specific plant and fungal species involved. For instance, *Epichloë coenophiala*, an endophytic fungus, colonizes tall fescue grass at its seedling stage, aiding its survival and growth (Zhang et al. 2017). Similarly, the nutrient-rich tissues of cacao trees during their reproductive stage attract a different set of endophytic fungi, like *Trichoderma* (López-Bucio et al. 2015). It is noteworthy that the composition of endophytic fungi communities is not static (Peršoh 2013). These communities can dynamically change over time as the plant matures and transitions through various growth stages. Understanding this temporal shift in endophyte communities is crucial for plant health, productivity, and ecosystem dynamics. Therefore, the study of endophytic fungi in young, rapidly growing plant tissues holds substantial importance in fields such as agriculture, forestry, and conservation biology.

(b) Mature Tissues

Mature plant tissues often have robust defenses, making them less susceptible to endophytic colonization. However, certain endophytes, for example, *Fusarium oxysporum*, may specialize in colonizing these tissues, either by overcoming the plant's defenses or by exploiting the resources available in mature tissues (Arnold et al. 2007, Gordon & Martyn 1997). Mature plant tissues indeed present a different environment compared to younger ones. They typically have robust defenses, which can make them less susceptible to colonization by endophytic fungi. Despite these defenses, some endophytes have evolved strategies to colonize these tissues by overcoming the plant's defenses or by exploiting the resources available in mature tissues. An example can be seen in pine trees (*Pinus* spp.), where certain endophytic fungi like *Rhizoscyphus ericae* have been found in mature tissues, including the roots. This fungus forms a mutualistic association with the host tree, aiding in nutrient uptake, particularly in nutrient-poor soils (Vrålstad 2004). Another example involves endophytic fungi in the genus *Neotyphodium* in perennial ryegrass (*Lolium perenne*) (Panaccione et al. 2006). These fungi persist in mature tissues, providing the grass with resistance against herbivores. The endophytes produce alkaloids toxic to insects and herbivores, helping to deter feeding (Saikkonen et al. 1998). These instances underline the dynamic nature of plant-endophyte interactions, particularly in mature tissues. The ability of endophytes to colonize and benefit from such an environment demonstrates their evolutionary adaptability and ecological significance. As such, a deeper understanding of these relationships can provide valuable insights for fields such as ecology, agriculture, and forestry, especially in strategies concerning plant health and productivity.

(c) Specific Developmental Stages

Certain endophytes might play crucial roles during specific stages of plant development. For example, some endophytes can promote seed germination, while others might enhance pollination success or protect flowers against pathogens (Hubbard et al. 2012, Doty 2017, Brody et al. 2019, Rana et al. 2019).

(1) Seed Germination

Some endophytic fungi can promote seed germination. For instance, a study found that endophytes belonging to *Ascomycota* improve wheat seed germination under heat and drought stress (Hubbard et al. 2012).

(2) Flowering

Endophytes can also enhance pollination success or protect flowers against pathogens (Rana et al. 2019). A study on Highbush blueberry (*Vaccinium corymbosum*) showed that the ericoid mycorrhizal fungi play a significant role in attracting pollinators by modifying floral scent compounds. This fungal endophyte indirectly affects the plant's reproductive success by enhancing pollinator visitation (Brody et al. 2019).

(3) Fruit Development

During fruit development, some endophytes may have a protective role. In tomatoes (*Solanum lycopersicum*), an endophytic fungus, *Fusarium solani*, has been observed to protect the fruit against another harmful fungus, *Botrytis cinerea*, which causes a disease known as gray mold (Kavroulakis et al. 2007, Sharma et al. 2009, Sinno et al. 2020). Overall, these examples underline the diverse and intricate roles that endophytic fungi play throughout a plant's life cycle. Their influences extend from the seed's earliest germination stages through the plant's maturity, contributing to the successful reproduction and health of the host. Understanding these relationships is crucial for the fields of agriculture and botany, where plant health, productivity, and successful reproduction are key objectives.

(d) Changes Over Time

The endophyte-plant relationship indeed mirrors the dynamism of a host plant's life cycle, with endophytic community composition and activity fluctuating over time. This results in a succession of different endophytic communities, each attuned to the conditions and challenges associated with a specific developmental stage. One pertinent example can be seen in maize (*Zea mays*) (Aamir et al. 2020). A study conducted by Liu et al. (2017) found that the endophytic fungal community in maize changed significantly across different growth stages. Specifically, the richness of the endophytic community increased from the seedling to the flowering stage but decreased at the fruiting stage. In a study conducted by Khan et al. (2016), the composition of fungal endophytic communities in phylloplane (leaf) and caulosphere (stem) of *Boswellia sacra* was found to change as the plant aged. The authors observed that the endophytic community structure was significantly different between seedlings and mature date palm trees. The study revealed that seedlings had a higher diversity of endophytic fungi, while mature trees exhibited a lower diversity but a higher abundance of certain endophytic fungi. This suggests that as the date palm matures, its interactions with endophytic community's change, reflecting the evolving needs and conditions of the plant throughout its life cycle. Early in development, plants might benefit from a broad diversity of endophytes that can enhance nutrient uptake or protect against pathogens. As the plant matures, specific endophytes that contribute to stress resistance or reproductive success might become more prevalent. The developmental stage of a plant significantly influences the presence, activity, and function of endophytic fungi. Understanding these dynamics can provide insights into the role of endophytes in plant growth and development, as well as the ecological and evolutionary pressures shaping endophytic communities.

4.6.4. Plant Health Status

(a) Healthy Plants

Healthy plants indeed possess a variety of physical and chemical defenses that serve as barriers to fungal colonization. The robustness of these defenses directly influences the ability of endophytic fungi to establish themselves within the plant tissue. Physically, the plant's cell walls form the first line of defense against invading fungi. They act as a physical barrier, making it difficult for potential invaders to penetrate into the plant's interior (Underwood 2012, Zeilinger et al. 2016). Furthermore, the plant's immune system plays a crucial role in recognizing and responding to potential fungal invaders. This system can detect pathogen-associated molecular patterns (PAMPs) and respond by triggering defense mechanisms that thwart the invasion e.g., Arabidopsis and cotton (Babilonia et al. 2021).

Chemically, plants produce a suite of antifungal compounds, such as phytoalexins, that inhibit fungal growth and development. This forms an essential part of the plant's innate immune response, particularly after the recognition of fungal PAMPs (van de Veerdonk et al. 2008, Bednarek & Osbourn 2009, Couto & Zipfel 2016). Moreover, a diverse and stable community of endophytes within a healthy plant can act as an additional layer of defense by outcompeting potential pathogenic fungi for resources (nutrients and space), effectively excluding them from colonizing the plant (Saikkonen et al. 1998, Niu et al. 2020). This unique ecosystem within the plant creates a selective environment that favors those endophytes that have either evolved mechanisms to overcome the plant's defenses or those that have developed a mutualistic relationship with the host, enabling them to coexist harmoniously with the plant and other resident endophytes (Rodriguez et al. 2009, Priyashantha et al. 2023).

Thus, a healthy plant, along with its resident endophyte community, forms a complex system that, under normal circumstances, can effectively ward off potential fungal pathogens. Recognizing these dynamics is essential to understanding plant health and disease and to devising effective disease management strategies.

(b) Stressed or Diseased Plants

Plant stress responses play an intricate role in the plant-endophyte relationship. A plant under various forms of stress – ranging from nutrient deficiency and water scarcity to exposure to extreme temperatures or pathogen attacks – may weaken its defensive mechanisms, rendering it more susceptible to colonization by endophytic fungi (Atkinson & Urwin 2012, Khoshru et al. 2020). These stressors can induce changes in the plant's physiology and biochemistry that are perceived by the endophytes, potentially influencing their behavior (van der Heijden et al. 2008). Stress can also lead to the production of specific volatile organic compounds (VOCs) or root exudates that serve as attractants to endophytic fungi (Plaszkó et al. 2020).

This increased attraction and colonization by endophytes under stress conditions may be part of a plant's adaptive response. By emitting certain signals, the plant may be 'calling' for assistance from beneficial endophytes to help combat the stressors or pathogens it is experiencing. This is in line with the "cry for help" hypothesis, which proposes that plants may recruit beneficial microbes to enhance their resilience in times of stress (Bazany et al. 2022, Trivedi et al. 2022). While, for example, endophytes like *Diaporthe liquidambaris* can switch to a pathogenic lifestyle if the plant's health continues to deteriorate (Zhou et al. 2018), others like the fungus *Penicillium resedanum* can provide valuable benefits, such as enhancing nutrient uptake, improving stress tolerance, and even producing anti-pathogen compounds to protect the host plant (Khan et al. 2015, Gouda et al. 2016, Elnahal et al. 2022). Understanding these dynamics can help us devise effective strategies for promoting plant health and disease management, especially under challenging environmental conditions. It also highlights the potential for using beneficial endophytes as biocontrol agents or biofertilizers in sustainable agriculture practices.

(c) Switching Lifestyles

The dynamic nature of endophytic fungi plays a substantial role in the overall health and resilience of the host plant. This characteristic of endophytic fungi is encapsulated in a concept known as the "endophyte-pathogen continuum," whereby these organisms can shift from a benign or beneficial existence within the host plant to a pathogenic one under specific circumstances (Rodriguez et al. 2009, Drew et al. 2021). These fungi can live in harmony with their host plant under optimal conditions, contributing to the host's overall health and offering various benefits such as enhanced nutrient uptake, protection against pests, and increased tolerance to environmental stressors (Rodriguez et al. 2009, Morand & Lajaunie 2017). They can further stimulate the production of plant secondary metabolites, aiding in the host's defense mechanism (Gouda et al. 2016, Pang et al. 2021).

However, when the plant's health deteriorates or when environmental conditions become unfavorable, these fungi can shift their lifestyle and become pathogenic. Environmental stressors, such as changes in temperature, humidity, nutrient availability, and exposure to toxins, can trigger this shift (Promputtha et al. 2007, Cavicchioli et al. 2019). Moreover, a weakened plant immune system can also provide an opportunity for endophytes to become pathogenic (Busby et al. 2016, de Lamo et al. 2021). Thus, understanding the triggers that lead to this shift from endophyte to pathogen is of utmost importance for managing plant health and disease. This knowledge could help in predicting disease outbreaks and implementing proactive measures, thus reducing reliance on reactive disease control strategies. Such insights also underscore the importance of maintaining optimal environmental conditions and plant health to preserve the beneficial role of endophytes and prevent their transition to a pathogenic lifestyle.

(d) Implications for Plant Health

The intricate interplay between a plant's health status and its associated endophytic fungi plays a vital role in plant health and disease management (Trivedi et al. 2020). Endophytes, which live within plant tissues without causing apparent harm, can be essential for the well-being of their host plant (Porras-Alfaro & Bayman 2011, Skinder et al. 2022). A balanced community of endophytic fungi is capable of conferring resilience against various environmental stressors and disease agents. They can help to enhance plant growth, promote nutrient uptake, and confer resistance against pests and pathogens (Rodriguez et al. 2009, Anand et al. 2023). A clear demonstration of this protective effect was observed in a study by Hardoim et al. (2015), where the researchers highlighted the importance of endophytic diversity in promoting plant health.

However, any alteration in this endophytic community – whether in terms of species diversity or the behavior of individual endophytes – can potentially lead to plant diseases. This is because different endophytes can either promote or inhibit the development of specific diseases, depending on their interactions with the plant and the pathogen involved (Busby et al. 2016). Therefore, any shift in the endophytic community, for example due to environmental changes, could disrupt this delicate balance and make the plant more susceptible to disease. Given these complexities, a profound understanding of these dynamics is fundamental for devising effective strategies to promote plant health and manage plant diseases. Knowledge about the specific roles of different endophytes in plant health, as well as how they interact with each other, with their host plant, and with potential pathogens, could be used to manipulate the endophytic community in ways that improve plant health and reduce disease incidence (Gouda et al. 2016, Pathak et al. 2022). To this end, further research in areas such as metagenomics and microbial ecology can shed more light on the intricate interplay between plants and their endophytic fungi, leading to more effective strategies for promoting plant health and managing plant diseases.

The health status of a host plant plays an instrumental role in influencing the evolution and behavior of endophytic fungi. This relationship is crucial in shaping the balance between beneficial and detrimental effects of endophytes on plant health, thus meriting further research for optimal management of plant health and disease control.

5. Future Directions

Considering the ecological and economic significance of endophytic fungi, comprehending their evolutionary origins and the factors driving their diversity and distribution is crucial. Future research should aim to integrate comparative genomics, experimental evolution, and ecological studies to unravel the complex evolutionary trajectories of endophytic fungi. Advancements in high-throughput sequencing and bioinformatics are expected to boost the exploration of endophyte diversity and function at an unprecedented scale, helping to decode complex host-endophyte interactions and expose the evolutionary forces that have shaped these relationships. Finally, the potential applications of endophytic fungi in sectors like agriculture, industry, and medicine require more exploration. By leveraging the unique capabilities of endophytes, we may find innovative solutions to pressing global challenges such as sustainable food production, environmental conservation, and disease management. Despite our significant progress in understanding the evolutionary history and ecological roles of endophytic fungi, there is still much to discover. The future of endophyte research is set to be a thrilling expedition of exploration and discovery.

6. Conclusion

The endophytic lifestyle in fungi, characterized by living within plant tissues often beneficially, is a highly adaptable trait that has evolved multiple times across various fungal lineages, driven by complex ecological and host-specific factors. This lifestyle, deeply rooted in the early colonization of terrestrial environments by plants, showcases the remarkable diversity and evolutionary flexibility of fungi. The study of endophytic fungi is crucial as it illuminates the intricate relationships between fungi and plants, and holds immense promise for practical applications in agriculture and pharmaceuticals through the development of biofertilizers, biopesticides, and discovery of novel medicinal compounds. Further multidisciplinary research employing genomic, ecological, physiological, and experimental approaches is imperative to unravel the complexities and potential applications of this vital component of biodiversity.

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Declarations

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential confict of interest.

Consent to participate

All authors have agreed to participate in this research.

Consent for publication

All authors have read and approved the submitted manuscript.

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