CHAPTER 6

Foliar Endophyte Communities and Leaf Traits in Tropical Trees

Sunshine Van Bael, Catalina Estrada, and A. Elizabeth Arnold

CONTENTS

6.1 INTRODUCTION

Tropical forests contain a great diversity of plant and fungal species. Plant–fungal interactions contribute to this richness, ranging in outcomes from pathogenic to mutualistic (Gilbert and Strong 2007; Rodriguez et al. 2009; Mangan et al. 2010). Although only a small fraction of tropical plant species has been assessed for foliar endophytes—fungi that live asymptomatically in leaf tissue—it has been suggested that foliar endophytes are hyperdiverse in tropical forests (Arnold et al. 2000; Zimmerman and Vitousek 2012). Understanding the factors that shape endophyte communities is important, given the diverse roles of endophytes in plant interactions with antagonists (Mejia et al. 2008), their effects on plant physiology (Arnold and Engelbrecht 2007; Mejía et al. 2014), and the potential of some endophytes to act as cryptic pathogens (e.g., Slippers and Wingfield 2007; Alvarez-Loayza et al. 2011; Adame-Álvarez et al. 2014). This chapter considers the degree to which theory applied toward understanding plant diversity applies also to fungal endophyte diversity, with an emphasis on encompassing factors such as functional traits and phylogenetic history in shaping tropical plant–symbiont interactions.

First, some mechanisms for community assembly and patterns of species coexistence are reviewed for plants and extended to fungal endophytes in temperate and tropical settings. Although data sets are somewhat restricted owing to potential culturing bias (Gallery et al. 2007; U’Ren et al. 2014), it appears that new leaves are flushed without endophytes (Arnold et al. 2003; Arnold and Herre 2003). Endophytes thus accumulate in leaves by horizontal transmission, analogous to colonization of bare resource patches by plants. We discuss how this parallels several recent theories on colonization and species coexistence from tropical forest plant communities.

Next, we explore the hypothesis that trade-offs in tropical plant life history strategies will lead to contrasting leaf traits that act as filters to shape the abundance, diversity, assembly, and composition of endophyte communities. Thus, while plant community assembly depends on environmental filters such as soil type or precipitation, leaves on those plants possess traits that constitute the “environmental filter” for endophytes that inhabit them. The concept of a “plant-imposed habitat filter” for fungal endophytes has been previously explored for crop plants and especially in the context of leaf chemical defense (see Saunders et al. 2010). Such ideas are extended here to encompass how plant trade-offs and associated functional traits may provide insight into patterns of abundance, diversity, assembly, and composition of endophyte communities in tropical trees.

Finally, we address how life histories of endophytic fungi and their associated functional traits may interact with plant life history traits. We view endophyte life histories in light of growth and colonization versus persistence trade-offs, consider how placing endophytism in a phylogenetic context reveals the close association of endophytes with pathogens, and discuss implications for understanding and predicting endophyte life histories.

6.2 COMMUNITY ASSEMBLY AND SPECIES COEXISTENCE

6.2.1 Plant Communities

Mechanisms of community assembly and species coexistence have been controversial topics in plant ecology, with widespread interest and debate fostering the growth of a robust body of theory. Early models for assembly, such as the climax model of succession (Clements 1916), treated plant community assembly as a deterministic trajectory, in which species are replaced sequentially to reach a stable state that is shaped by environmental factors. Alternatively, historical or “priority” effects were viewed as the basis for stochastic models in community assembly (Gleason 1926; Diamond 1975). In these models, plants arriving first to a bare resource patch will modify the subsequent plant community via competition or by changing soil properties (i.e., soil legacies [Grman and Suding 2010]).

More recent models for species coexistence include a dichotomy of deterministic and stochastic mechanisms, including niche-based theories, neutrality-based theories, and syntheses of these (Tilman 2004). Niche-based theory suggests that interspecific variation in ecological traits of species (i.e., deterministic trait variation) allows limited resources to be partitioned among competitors (Chase and Leibold 2003). In this framework, niche space is defined by biotic interactions based on species traits and/or environmental filtering. For example, environmental filtering occurs if temperature, precipitation, or soil characteristics preclude a certain set of plant species while favoring another. In contrast, theory based on neutrality focuses on dispersal limitation and neutrality in traits, predicting that changes in species composition will be related to stochastic events or shaped primarily by geographic distance (MacArthur and Wilson 1967; Hubbell 2001). In this scenario, plant species are assumed to be ecologically equivalent and to have consistent demographic rates (Hubbell 2001; Chave 2004).

Contrasting bodies of theory in plant ecology posit mechanisms that are not mutually exclusive; in fact, syntheses such as “stochastic niche theory” (Tilman 2004) combine niche/trait factors with stochastic dispersal limitation. In general, it is thought that plant communities are likely to be structured by interactions among spatial, ecological, and evolutionary forces (Leibold et al. 2004), with support from recent meta-analyses (e.g., a meta-analysis of community studies revealed that 44% of communities showed signs of species sorting or environmental filtering, 29% showed a combination of environmental and dispersal effects, and 8% showed spatial factors that reflect neutral processes; Cottenie 2005).

AQ 1

6.2.2 Fungal Endophyte Communities

How do assembly and coexistence models based on plants and other organisms reflect the assembly and structure of fungal endophyte communities? Like many plants, endophytes may be subject to dispersal limitation. Airborne or waterborne propagules may spread passively. Endophytes often coexist with one another in shared habitats (i.e., within leaves), and priority effects that influence the ultimate composition of fungal communities have been detected (Adame-Álvarez et al. 2014). However, the cornerstones of niche-based theory—which often rest on functional traits—are not yet well established for endophytes, and the close relationship of endophytes with pathogens suggests that in many cases, host responses that favor particular fungi over others may preclude purely neutral processes in endophyte community establishment. Thus, the relative importance of niche- and neutrality-based processes in shaping endophyte communities has not been explored in detail. Here, we highlight recent areas of inquiry that can inform the factors influencing endophyte community assembly.

Competition among species is at the foundation of niche-based theory (Chase and Leibold 2003). Many traits of fungal endophytes suggest that they are equipped to compete with other microbes, and several studies have identified distribution patterns in nature, *in vitro* traits, and interactions in symbiosis that are consistent with competition (Arnold et al. 2003; Pan and May 2009; Saunders et al. 2010; Adame-Álvarez et al. 2014). Both direct competition and/or antagonism (as mediated by fungal secondary metabolites; see below) and competition that may indirectly involve plant defenses (e.g., upregulation of defenses; see below) may be important, though their relative contributions to endophyte assembly are not yet well known.

In parallel with competition, endophyte community assembly involves filters at several spatial and biological scales. Saunders et al. (2010) reviewed studies of fungal endophytes in crop plants to develop a community assembly model in which endophyte spores begin as part of a regional species pool and then disperse through a series of filters consisting of (1) abiotic factors (such as temperature, humidity, and ultraviolet radiation), (2) plant traits, and (3) competitive filters (i.e., microbial species interactions) (Saunders et al. 2010). These processes work at different scales and are not mutually exclusive or necessarily nested (Saunders et al. 2010). The strongest empirical support for plant-trait filtering came from differences in maize genotypes with differential production of secondary defense compounds (Saunders and Kohn 2009). Maize genotypes that produced defensive compounds supported endophyte communities that demonstrated a relatively greater level of tolerance to host toxins (Saunders and Kohn 2009). These results are complemented by leaf-extract assays by Arnold and Herre (2003) and Lau et al. (2013), who found strong effects of host versus non-host leaf chemistry on endophyte growth *in vitro*. Huang et al. (2015) found that endophyte abundance, diversity, and composition were not strongly influenced by intraspecific variation in leaf nutrients such as Ca, Mg, K, and N, suggesting a strong role of leaf phenology or defensive chemistry in filtering endophyte assemblages. In turn, evidence for the importance of microbial interactions has been inferred when endophyte communities show nonrandom co-occurrences across host genotypes (Pan and May 2009). Similarly, other fungal endophyte studies have suggested that host traits or host taxonomy may be key drivers for determining community structure (Arnold et al. 2003; Helander et al. 2007; U'Ren et al. 2009; Sanchez-Azofeifa et al. 2012). These studies echo growing evidence from other functional groups of plant-associated fungi, which reveal the importance of host traits and taxonomy for structuring fungal pathogen communities (Gilbert and Webb 2007), mycorrhizas (Dumbrell et al. 2010), and epiphytic fungi on leaves (Kembel and Mueller 2014).

Shifting from the internal leaf environment to the ambient environment, several studies of fungal endophytes across environmental gradients have offered insight into how abiotic environmental filtering influences endophyte community assembly and structure. One example showed that leaf endophytes on Mauna Loa (Hawaii) formed very distinct communities along an elevation, temperature, and precipitation gradient, with the greatest diversity at low elevation sites (Zimmerman and Vitousek 2012). Similarly, foliar endophytes in grasses showed strong species sorting with respect to a rainfall gradient in Central Texas (Giauque and Hawkes 2013). At a continental scale, U'Ren et al. (2012) showed that rainfall and temperature are important determinants of community similarity. Environmental filtering by bedrock/soil type shapes communities of endophytes in roots of Arctic plants (Blaalid et al. 2014). For tropical woody species, fungal endophyte communities along environmental gradients (such as precipitation gradients) have been studied rarely (Suryanarayanan et al. 2002) and need to be explored further.

Although studies with crops and environmental gradients point strongly to niche-based mechanisms, other examples highlight the potential for stochastic and/or priority effects (e.g., Helander et al. 2007). One recent study showed very little host or site specificity of horizontally transmitted foliar endophytes in tropical grasses (Higgins et al. 2014). Instead, widespread host-sharing and strong spatial structure in endophyte communities was consistent with dispersal limitation (Higgins et al. 2014). Whether such patterns hold for trees as well as grasses in tropical forests requires spatially explicit work on these diverse communities, but the prevalence of dispersal limitation in many fungal guilds is compelling (e.g., fungi in indoor air, Adams et al. 2013; soil microbes, Peay et al. 2010; and temperate endophytes inhabiting conifer needles, Oono et al. 2014). Recent work in paleotropical rainforests suggests a stronger effect of host species than that of dispersal limitation in structuring endophyte communities (Vincent et al. 2015). Evidence for priority effects has been demonstrated with serial inoculations of endophytic and pathogenic fungi (Adame-Álvarez et al. 2014), among mycorrhizas and root endophytes (Eschen et al. 2010, Rillig et al. 2014), and for fungal endophyte–endophyte interactions (Pan and May 2009). Priority effects among fungal endophytes in diverse settings require further study to make generalizations for tropical plants.

Overall, endophyte studies provide examples of niche-based and neutral/stochastic scenarios for community assembly and species coexistence. As described above, evidence of niche-based processes is more common in the literature than examples consistent with strictly neutral processes. This difference could indicate that researchers are rarely placing their endophyte work in the spatially explicit framework needed to observe patterns of neutrality. The goal of estimating global fungal abundance has led to endophyte sampling regimes that have focused more on determining host specificity and less on niche-based versus neutral processes. Host taxonomy is likely an important indicator of endophyte community structure, but even within very closely related host species, species-specific plant traits can vary. For example, several recent studies in lowland tropical plant communities have shown that plant's defensive traits vary dramatically among congeneric species, with no clear phylogenetic signal (Kursar et al. 2009; Sedio 2013). Thus, a closer look is warranted at how leaf traits influence foliar endophyte communities in species-rich plant communities.

6.3 TRADE-OFFS AND LEAF TRAITS

Plant life histories and associated traits are shaped by biotic and abiotic influences in both ecological and evolutionary time frames (Ackerly and Reich 1999; Westoby 2002; Nicotra et al. 2011; Adler et al. 2014; Broadbent et al. 2014; Price et al. 2014; Muscarella et al. 2015; Blonder et al. 2016). AQ 2 In the understory of seasonal tropical forests, for example, annual changes in precipitation influence plant growth and traits directly by driving water availability (Wright and

AQ 3 Cornejo 1990; Lüttge 2007; Craven et al. 2011; Lee et al. 2013). At the same time, biotic interactions with pathogens and herbivores shape plant defense and persistence (Coley and Barone 1996), often interacting with environmental conditions such as light, precipitation, and other seasonal factors that shape biotic interactions (e.g., life style shifts in fungal–plant associations, Alvarez-Loayza et al. 2011, and effects on density-dependent regulation of plant community structure, Bunker and Carson 2005; see also Novotny and Basset 1998; Pinheiro et al. 2002; Sloan et al. 2007; Lin et al. 2012; Van Bael et al. 2013; Piepenbring et al. 2015).

"Growth versus persistence" (or defense) constitutes a key trade-off for describing plant communities in tropical forests (Poorter and Bongers 2006; Kitajima et al. 2013). Although many whole-plant traits such as wood density and seed size contribute to the growth versus persistence trade-off (Swenson and Enquist 2007; Adler et al. 2014), leaf traits such as leaf life span, thickness, mass, and nutrient content are useful indicators for describing plant life history strategies (Westoby 2002). Plant species in tropical forests exhibit the growth versus persistence trade-off by producing short-lived, fast-growing leaves with few structural or chemical defenses versus long-lived, slow-growing leaves with more investment in defense (Poorter and Bongers 2006; Kitajima et al. 2013). In the carbon balance hypothesis, a longer leaf life span allows species in low light, poor soils, or with limited physiological capacities to accumulate more carbon from each individual leaf (Chabot and Hicks 1982; Givnish 2002). Long-lived leaves also use nutrients more efficiently than leaves with shorter life spans (Chabot and Hicks 1982). Global data sets have been used to show the existence of a leaf economics spectrum, in which six leaf traits reliably explain the investment-to-return rate in leaves (leaf life span, leaf nitrogen and phosphorous, photosynthetic and dark respiration rates, and leaf mass per area [LMA]) (Wright et al. 2004).

We posit that the growth versus persistence trade-off and related leaf traits are important in shaping foliar endophyte communities. Endophytes are defined functionally by their occurrence, for at least part of their life cycles, within living, symptomless plant parts (*sensu* Class 3 endophytes, Rodriguez et al. 2009). Thus, endophytic fungi must interact with leaf traits in several stages of the life cycle. Such interactions include adhesion to leaf surfaces and/or initial colonization of living leaves; persistence within living leaves, despite the potential to consume foliar carbon (a high cost AQ 4 in carbon-limited forest understories; Veneklaas and Poorter 2006) and the prevalence of antifungal defenses (e.g., Kursar and Coley 2003); and the ability to disperse, typically from senescent leaves or insect frass, following herbivory (Monk and Samuels 1990; Devarajan and Suryanarayanan 2006; AQ 5 Promputtha et al. 2007; Arnold 2008; Vega et al. 2010). Because endophytes typically occur as part of rich microbial communities on leaf surfaces and within leaf tissues, their interactions with co-occurring microbes—, which may in turn be driven, by the interaction of environment, phylogeny, and functional traits—are also important in shaping endophyte assemblages in the phyllosphere.

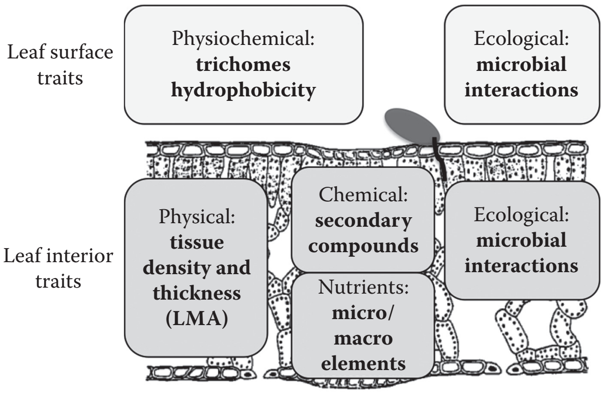

Figure 6.1 Leaf traits that may influence fungal endophyte colonization and persistence in leaves of a tropical forest understory.

Generally, more is known about fungal pathogen–leaf interactions than about endophyte–leaf interactions. Most commonly isolated endophytes are closely related to pathogenic strains (Arnold et al. 2009; García-Guzmán and Heil 2013), such that perspectives may be extended from pathogens to closely related endophytes. Both fungal pathogens and fungal endophytes interact with physiochemical traits on leaf surfaces, physical and chemical traits in the leaf interior, and microbial communities on the leaf surface and interior (Figure 6.1). Finally, these leaf traits are not static: they differ dramatically for young, expanding leaves relative to mature leaves. In general, empirical studies are needed to understand microscale processes of leaf colonization, interactions with other trophic groups, the relevance of biotic and abiotic stress in context-dependent colonization, and metabolome/transcriptome-level responses to colonization (see Mejía et al. 2014).

6.3.1 Leaf Colonization and Physiochemical Surface Traits

Data to date suggest a prevalence of horizontal transmission among fungal endophytes of tropical leaves (e.g., Arnold and Herre 2003). Culture-based methods should be complemented by culture-free methods (e.g., Pan and May 2009; U'Ren et al. 2014) to confirm the endophyte-free status of young leaves and thus to shed light on potential vertical transmission in tropical endophyte communities. In general, very little is known about how endophyte spores and hyphae interact with leaf surface and interior traits in tropical plants. Leaf surfaces are complex, with variation occurring among plant species and cultivars, and even within plants (Allen et al. 1991). When a pathogenic or endophytic fungal spore lands on a leaf surface via rain splash, the spore is likely influenced by leaf surface traits, such as trichomes and wax crystals, that determine the physical leaf surface and confer hydrophobicity or leaf water repellency (Holder 2011). Trichomes, or hairy extensions from the leaf surface, may trap the water and spores or may prevent spores from reaching the leaf surface (Allen et al. 1991). Some trichomes also produce chemicals that deter herbivores and influence penetration success of fungal spore for pathogens and endophytes (Valkama et al. 2005). Trichome abundance may act to negatively influence endophyte spores on leaf surfaces and decrease their penetration; however, they may also provide a route of entry for fungi. For instance, Bailey et al. (2009) showed that some endophytic *Trichoderma* associate with glandular trichomes of *Theobroma cacao.* Mucciarelli et al. (2002) showed that dense mats of anastomosed hyphae appressed to the leaf cuticle were associated with colonization of *Mentha* leaves.

Leaf drainage patterns may negatively influence spore survival and endophyte entry into the leaf. The quantity and arrangement of wax crystals in the cuticle influence hydrophobicity and can result in water draining off the leaf surface and “cleaning” it of spores (Martin and Juniper 1970). Most fungal spores that land on a leaf surface require water in order to germinate and then punch a penetration peg through the leaf surface, while other types of fungal pathogens and some endophytes enter the leaf via stomata (Carlile et al. 2001; Johnston et al. 2006; Mejia et al. 2008; Melotto et al. 2008), with stomatal regulation by metabolites such as oxalic acid known in diverse fungal taxa (Gudesblat et al. 2009). In the growth versus persistence trade-off, trichomes and thick, waxy cuticles generally correlate positively with AQ 6 leaf mass per area (LMA) and leaf life span and are thought to act as defensive traits with respect to herbivores and pathogens (Valkama et al. 2005).

Finally, Arnold (2008) reported an increase in isolation frequency and diversity of endophytes from leaves of *Gustavia superba* in Panama, following leaf damage by hesperid caterpillars, consistent with a potential role of herbivores in introducing some endophytes and a potentially limited capacity of induced responses to herbivory (e.g., jasmonic acid [JA]) to limit endophyte entry or proliferation (see also Faeth and Wilson 2002; Humphrey et al. 2014).

6.3.2 Physical Leaf Traits

Once inside the leaf, fungal hyphae typically grow into the intercellular spaces of the mesophyll or the apoplast (see *Cladosporium* in Giraldo and Valent 2013; see also Clay 2001; Johnston et al. 2006). Given the need to extend hyphae through the mesophyll, it is possible that endophyte movement is constrained by tissue density, with greater colonization of endophytes taking place where tissue is less dense. Leaf mass per area (LMA) is a product of leaf thickness and tissue density and correlates with leaf life span, such that thicker, denser leaves tend to live longer (Poorter and Bongers 2006; Lamont et al. 2015; Tozer et al. 2015). One prediction is that endophyte density inside leaf tissue will correlate negatively with increasing LMA, since denser leaf tissue may restrict endophyte hyphal growth (Nezhad and Geitmann 2013). Entrance into the leaf is likely easier in thinner, less dense leaves (Arnold and Herre 2003). Leaf blade thickness increases with higher light levels as a result of increasing the thickness of the palisade layer (Ashton and Berlyn 1992), suggesting that endophyte abundance may be lower in high-light leaves compared with low-light leaves.

6.3.3 Nutrients

Nutrients in leaves and soil have the potential to influence foliar endophytes. In one study, sulfur, nitrate, and calcium citrate content in leaves correlated with endophyte community differences (Larkin et al. 2012). In contrast, Huang et al. (2015) found no correlations among foliar Ca, K, Mg, and N and endophyte abundance or diversity for one host species, while foliar Mg and N were negatively correlated with endophyte abundance for another host species. In leaves that were inoculated with one common tropical endophyte, positive correlations for endophyte abundance and Al, Ca, and Fe were observed (Estrada et al. 2013). Soil nutrient concentrations can influence leaf traits and leaf foliar nutrient concentrations. Soil type and microhabitat are demonstrably important in shaping plant traits and root-associated fungi (e.g., Corrales et al. 2015), but evidence generally suggests that foliar endophytes are rarely structured by soil type over short geographic distances (e.g., Higgins et al. 2014; see also Ren et al. 2015; but see Eschen et al. 2010).

6.3.4 Chemical Leaf Traits

The ability to colonize leaf tissues by fungi is determined in large part by complex chemical interactions with their hosts. Fungi must resist host production of antimicrobial compounds, and the plant–fungal interaction may also include molecular cross-talk, manipulation, and deception (Chisolm et al. 2006; Christensen and Kolomiets 2011; Mengiste 2012; Kusari et al. 2012). The use of crop–pathogen models has been helpful in understanding what makes some plants resistant to fungal infections. Much less is known about which chemical environments within the host allow symbiotic fungi to remain asymptomatic or how rich communities of fungi with endophytic life styles coexist in leaves for long periods of time. Patterns of genetic and phenotypic expressions of plants infected with endophytes show that colonization by these symbionts is recognized by the plant and triggers immune responses that are to some degree similar to those produced by pathogens and other microbial symbionts (e.g., rhizobium bacteria and mycorrhizal fungi) (Schulz and Boyle 2005; Zamioudis and Pieterse 2012; Hartley et al. 2014; Mejía et al. 2014; Foster et al. 2015).

Plant responses to fungal colonization are predominantly determined by fungal nutritional strategies (e.g., biotrophic, necrotrophic, and hemibiotrophic). Plants respond to biotrophic and hemibiotrophic pathogens by activating the salicylic acid (SA)-dependent signaling pathway that triggers a localized programmed cell death in resistant hosts; this cell death inhibits fungal growth (Chisholm et al. 2006). Resistance to necrotrophic fungi and herbivores depends on signaling pathways activated by ethylene (ET) and jasmonic acid (JA). These hormones regulate the expression of genes associated with cell wall defense, protease inhibition, and synthesis of antimicrobial secondary metabolites (Mengiste 2012). The SA and JA/ET defense pathways are mutually antagonistic, a feature that is often exploited by pathogenic microbes to suppress host resistance (Chisholm et al. 2006; Mengiste 2012). The well-studied clavicipitaceous endophytes, mutualists of pooid grasses, are closely related to species with biotrophic nutrition; these endophytes share an ancestor that was likely an arthropod pathogen (Spatafora et al. 2007). However, non-clavicipitaceous leaf endophytes are often related to fungal species with a necrotrophic or hemibiotrophic life style, some of which establish transient asymptomatic infections (Münch et al. 2008; Delaye et al. 2013; García-Guzmán and Heil 2013). Moreover, endophytes that shift to a parasitic life style after changes of host physiology (e.g., development and stress) often induce necrosis (Guetsky et al. 2005; Alvarez-Loayza et al. 2011; van Kan et al. 2014).

Consistent with their origin, recent studies show that Class 3 leaf endophytes activate parts of the JA and ET signaling pathways in their host; however, the extent to which these defenses contribute to the fungal asymptomatic life style are still unknown. In particular, plants infected with one endophyte strain have shown higher expression of genes associated with ET signaling in *Theobroma cacao* (Mejía et al. 2014) and higher concentration of oxylipin metabolites that are part of the JA signaling pathway in *Cirsium arvense* (Hartley et al. 2014). Emissions of JA and volatile compounds associated with this hormonal pathway have been shown to also increase in leaves colonized by some endophyte strains but not others (Mucciarelli et al. 2007; Ren and Dai 2012; Estrada et al. 2013; Navarro-Meléndez and Heil 2014). Moreover, according with the JA–SA pathway trade-off, endogenous levels of SA are reduced during leaf endophyte colonization (Navarro-Meléndez and Heil 2014). Colonization of leaves by endophytic fungi also caused upregulation of genes involved in signaling and cell wall modification, as well as phenotypic changes that include deposition of lignin, cellulose, and callose (Johnston et al. 2006; Mejía et al. 2014; Busby et al. 2015).

AQ 7

Regardless of their life style, fungi must have the ability to evade the action of the basal plant immune system to successfully colonize a leaf. The plant's first response to microbial infection is activated by conserved microbial features (microbe-associated molecular patterns [MAMP]) or early symptoms of tissue damage (damage-associated molecular patterns [DAMP]) (Chisholm et al. 2006; Mengiste 2012). Typically triggered plant responses include production of chitinases to degrade fungal cell walls, reinforcement of the plant cell wall, production of reactive oxygen species (ROS, e.g., hydrogen peroxide and hydroxyl radical) that are both toxic and work as signaling molecules, the activation or mobilization of preformed antimicrobial metabolites (phytoanticipins), and the synthesis and accumulation of de novo toxic compounds (phytoalexins) (Mittler et al. 2004; Bednarek and Osbourn 2009; Mengiste 2012; Foster et al. 2015). Successful necrotrophic pathogens avoid these basal defenses and induce cell death. This might involve the production of phytotoxic metabolites or the activation of an oxidative burst, which often requires triggering the expression of plant responses against biotrophic pathogens (e.g., induction of programmed cell death). Consequently, mechanisms that prevent fungal manipulation and evade the action of toxins contribute to host resistance (van Kan 2006; Mengiste 2012). It is still unknown which partner has the control or which mechanisms maintain the interacting species in the "balanced antagonism" that results in long lasting, asymptomatic infections of leaves (Schulz and Boyle 2005; Kusari et al. 2012; van Kan et al. 2014). Research on pathogens and root microbial mutualists suggests that such mechanisms might be as diverse as the species implicated and the environmental context of the interactions.

The importance of plant secondary metabolites as a mechanism influencing the success of fungal colonization and shaping the assemblages of endophyte communities is well known (Schulz and Boyle 2005; Saunders and Kohn 2009; Fernandes et al. 2011). This aspect of the plant immune system is implicated in maintaining infections asymptomatic or quiescent; and with reductions in antifungal levels often correlated to the development of diseases (Mansfield 2000; Guetsky et al. 2005). Successful symbionts counter host antifungal compounds by common mechanisms that include evasion, tolerance, and detoxification (Pedras and Ahiahonu 2005; Saunders et al. 2010; Pedras and Hossain 2011; Díaz et al. 2015). One endophytic species from leaves of the medicinal plant *Cephalotaxus harringtonia* goes even further when it activates its host's glycoside metabolites by removing the sugar molecules and releasing the corresponding flavonoid aglycones (Tian et al. 2014). These compounds promote the endophyte's own hyphal growth and are expected to influence negatively the colonization by other fungi (Tian et al. 2014). This ability to counter plant defensive compounds differs considerably among fungal species (Saunders et al. 2010). Thus, leaves with high content of secondary metabolites are expected to host lower densities of endophytes and/or to host communities dominated by a few species that are well adapted to deal with particular defensive compounds.

AQ 8

Given that investment in secondary metabolites is a predictable defensive trait across tropical plant species, and through leaf development, it may be possible to predict the similarity of leaf endophyte communities at local spatial and temporal scales. For instance, greater similarity is expected among communities hosted by mature leaves, particularly the long-lived leaves from slow-growing plants, which typically invest relatively more in structural defenses than in secondary metabolites (Kursar and Coley 2003; Kursar et al. 2008; Endara and Coley 2011; Bixenmann et al. 2013; García-Guzmán and Heil 2013). Likewise, among young leaves, those with rapid expansion rates (Kursar and Coley 2003) and low levels of secondary metabolites are expected to be colonized by generalist endophytes that are locally abundant. These predictions are borne out in age-structured surveys of leaves (e.g., Arnold et al. 2003).

6.3.5 Ecological Interactions

Endophytes interact with the large, dynamic, and diverse microbiome present on leaf surfaces (see Vorholt 2012), including diverse fungi and bacteria in tropical forests (Kembel and Muller 2014; Kembel et al. 2014; Griffin and Carson 2015). Endophyte propagules may antagonize or encourage growth by other phyllosphere microbes. For example, propagules may produce or alter metabolites, provide structural complexity, compete for space and resources, and alter leaf-surface trophic webs (e.g., Blakeman and Fokkema 1982).

Inside the leaf, endophytes may be further influenced by fungal or bacterial endophytes that are already present. Microbial influences could be indirect, via their effects on plant defenses and the chemistry of leaves, or direct, due to interspecific microbial interactions (Arnold et al. 2003; Saunders et al. 2010; Friesen et al. 2011; Gange et al. 2012; Adame-Álvarez et al. 2014; May and Nelson 2014s; Mejía et al. 2014). Evidence that these interactions are crucial for fungal colonization comes from negative relationships in the abundance of common species (Pan and May 2009) and from observations that endophytes can either reduce or increase the severity of pathogenic infections (Arnold et al. 2003; Rodriguez Estrada et al. 2012; Busby et al. 2013; Raghavendra and Newcombe 2013; Busby et al. 2015).

The production of secondary metabolites by fungal endophytes may be aimed specifically at microbes that reside in the same tissues (Kusari et al. 2012; Soliman and Raizada 2013). For example, when growing in cocultures, both endophytic bacteria and fungi secrete antimicrobial compounds that show toxicity toward each other (Chagas et al. 2013; Schulz et al. 2015). Similarly, a maize endophyte produced secondary metabolites in the presence of a fungal pathogen; the secondary metabolites resulted in a growth benefit for the endophyte and growth reduction for the pathogen (May and Nelson 2014). Secondary metabolites that serve as signaling molecules can also manipulate the metabolic pathways of other microbes (Kusari et al. 2012). Lipid-derived oxylipins are molecular signals that mediate plant–fungal and interspecific microbial communication. In fungi, oxylipins have been implicated in regulation of mycotoxin production, quorum sensing, and fungal reproduction (Christensen and Kolomiets 2011). For example, in a mixed culture with *Fusarium oxysporum,* the endophyte *Paraconiothyrium variabile* produced two metabolites from the oxylipin family that were presumably related to the reduction of mycotoxins by *Fusarium* (Combès et al. 2012). Some metabolites of endophytes may be produced only in the presence of particular substrates or plant-produced compounds, which may in turn be host-specific. A frontier in this area of inquiry lies in using plant- or microbially produced compounds as epigenetic modifiers to diversify and intensify secondary metabolite production by fungi (see Williams et al. 2008; Chiang et al. 2009; Cichewicz 2012; Demers et al. 2012; Chen et al. 2013; Takahashi 2014).

Thus, ecological interactions *in planta* may lead to a “balanced antagonism,” wherein interspecific interactions among microbes form a multipartite symbiosis that benefits the plant hosts’ immunity toward pathogens (May and Nelson 2014; Schulz et al. 2015). All leaves in tropical forests are susceptible to fungal pathogens to different degrees. However, longer-lived leaves may rely on intrinsic defense, while shorter-lived leaves may rely more on the acquired defense of ecological interactions among endophytic symbionts.

6.3.6 Leaf Expansion Rates and Coloration

Tropical tree species vary widely in rates of leaf expansion, and the leaf expansion period may be most vulnerable stage during the life of the leaf (Coley and Kursar 1996). For tropical woody species in the understory, young expanding leaves suffer 5 to 100 times the damage from pathogens and herbivores as mature leaves (Coley and Aide 1991). As expansion rate is a trait that influences fungal pathogens; it also likely affects the community assembly of fungal endophytes. The changes that occur in leaves during the expansion period encompass traits from many of the categories described above; physical, chemical, and nutritional differences are observed between young and mature leaves (Coley and Kursar 1996). In particular, young, expanding leaves are soft relative to tougher, older leaves. Cuticular penetration is likely easier in expanding leaves that have not become tough, just as it is easier for herbivores and fungal pathogens to damage or infect young leaves. However, Arnold and Herre (2003) found no difference in cumulative infection rates in old versus young leaves of cacao, despite differences in toughness and chemistry as a function of leaf life stage. Leaf expansion rate has not been considered part of the growth versus persistence trade-off; however, delayed greening during leaf expansion showed a trend toward a positive correlation with longer leaf life span on Barro Colorado Island, Panama (Coley and Kursar 1996).

The red or pale coloration of tropical leaves during the leaf expansion period may also influence endophyte community assembly. In particular, many tropical species flush entire canopies of red- or pale-colored leaves that turn green only on maturation of the leaf (Coley and Kursar 1996; Dominy et al. 2002). Anthocyanins are compounds that cause red coloration of expanding leaves. Anthocyanins have been shown to confer antifungal effects for tropical AQ 9 leaves (Coley and Aide 1995; Tellez et al. 2016). Thus, expanding leaves with red coloration may have a delay in assembling their fungal endophyte communities relative to leaves with lower anthocyanin content. With respect to the growth versus persistence trade-off, red coloration has been shown to correlate positively with a persistence strategy and negatively with seedling growth (Queenborough et al. 2013).

In summary, leaf trait syndromes reflected in the growth versus persistence trade-off are predicted to constrain fungal endophytes. These constraints include physio-chemical barriers to leaf entrance, the growth of hyphae in the apoplast, interactions with plant secondary compounds, competition/facilitation by other microbes on leaf surfaces and interiors, and leaf development traits. Given the endophyte-leaf interactions discussed above, it is predicted that endophytes will correlate positively with a "growth strategy" and negatively with a "persistence" strategy. Thus, endophyte abundance and diversity are predicted to be greater, in short-lived leaves relative to long-lived leaves.

6.4 ENDOPHYTE LIFE HISTORY AND FUNCTIONAL TRAITS

Endophytes' life history is strongly influenced by their small size, short generation times (relative to plants), and their occurrence, for at least part of their life cycles, as internal symbionts of leaves (Rodriguez et al. 2009). From the endophyte's perspective, inhabiting a leaf with a shorter leaf life span may be preferable to colonizing a longer-lived leaf; because endophytes generally reproduce at leaf senescence and abscission, selection may favor endophyte colonization of short-lived leaves (see also Arnold et al. 2009). In some cases, endophyte reproduction and dispersal of spores occur in insect frass (Monk and Samuels 1990). Because chewing insects frequently prefer leaves with growth-oriented versus persistence traits, endophytes would shorten their route to reproduction by colonizing rapidly growing leaves with short life spans. In such a scenario, endophytes could be selected to facilitate herbivory by chewing insects (Cheplick and Faeth 2009). In turn, effects on other herbivores (e.g., sucking insects) might be predicted to be AQ 10 more diffuse. Connections between endophytic fungi and insects are not only widespread in terms of potential roles in dispersal but also entomopathogenic in ecological time (Vega et al. 2010) and over evolutionary history (see Spatafora et al. 2007; Zhao et al. 2014).

Just as in plants, fungal endophytes may develop life histories that are constrained by trade-offs in growth versus persistence. Fungal endophyte species may grow rapidly, emphasizing hyphal extension and resource competition over persistence traits. These fungi may be host generalists, analogous to many saprotrophs, and particularly straightforward to isolate in culture on standard media. When studied using culture-based methods, tropical endophyte communities are often rich in fungi that fall on the endophyte-saprotroph continuum (e.g., *Xylaria*). In contrast, a persistence strategy might include traits such as toxin or antibiotic production. Antibiotic production could lead to favorable outcomes for certain types of competition with other endophytes. Moreover, a successful persistence strategy via antibiotic production may prevent host leaf tissue from being invaded by fungal pathogens or mycoparasites (Arnold et al. 2003; Saunders and Kohn 2009). It is a challenge to assess a growth versus persistence strategy for endophytes, because endophytes are generally studied only in culture and it is difficult to extend *in vitro* results to *in planta* interpretations. Moreover, fungi that appear to follow the rapid-growth strategy also produce potent metabolites (e.g., cytochalasins and sesquiterpenes, produced by *Xylaria;* Jimenez-Romero et al. 2008; Xu et al. 2015; Wei et al. 2016). Fungal growth and AQ 11 competition behavior *in vitro* depend on the culture media used, and adding extracts of the plant host to the cultures can change the outcome of fungal growth and of fungal-fungal interactions (Arnold et al. 2003; Arnold and Herre 2003). Nonetheless, a few studies have illustrated how metabolites produced by fungal cultures are also detected from plants inoculated with those same fungal endophytes (Aly et al. 2008; Xu et al. 2009; Aly et al. 2011).

One prediction is that fungal endophyte life histories will "track" the life histories of their host plants; that is, endophytes with a life history that emphasizes rapid growth will be more likely to colonize rapidly growing leaves with short life spans, while slowly growing endophytes can more effectively colonize and compete inside the leaves with longer life spans. If this is true, we would expect to see greater production of defensive compounds (i.e., antibiotics) in slow-compared with fast-growing endophytes.

A useful tool in diagnosing endophytes' interactions and predicting aspects of their functional traits may lie in the evolutionary history of endophyte species. Although endophytes are frequently absent from large-scale reconstructions of fungal evolution, several studies have explored the evolutionary origins of endophytism in a phylogenetic framework (see Spatafora et al. 2007; Arnold et al. 2009; U'Ren et al. 2009; García-Guzmán and Heil 2013). The latter studies focused on horizontally transmitted endophytes and included strains from tropical plants. In the context of the most species-rich fungal phylum (Ascomycota), the authors reconstructed ancestral states on a three-locus tree,

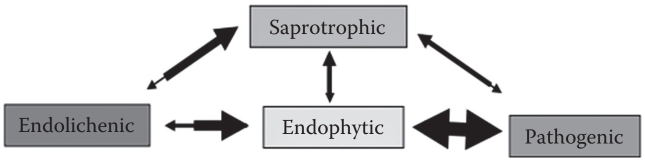

Figure 6.2 (**See color insert.**) Proposed directionality and frequency of evolutionary shifts in the Ascomycota, revealing multiple evolutionary origins of endophytic fungi. Thickness of arrows is proportional to transition frequency; modified from Arnold et al. (2009) and U'Ren et al. (2009). Understanding the phylogenetic history of endophyte species may provide tools to estimate their genomic architecture (increasingly capable of mitigating or evading plant defenses from left to right and top to bottom), infection strategy (increasingly active from left to right), potential host breadth (decreasing from left to right), and expected traits in symbiosis (growth rate increasing left to right and bottom to top; life span decreasing left to right and bottom to top).

incorporating observations of life history and records of host use/ecological modes from the literature. Figure 6.2 summarizes these findings.

In general, a strong evolutionary connection was observed between endophytic and pathogenic life styles, consistent with colonization and growth within living plant tissues. Such transitions were observed among some of the common Dothideomycetes, Sordariomycetes, and Eurotiomycetes, frequently found in tropical plants as endophytes (e.g., in *Botryosphaeria, Mycosphaerella,* and diverse Pleosporales; the *Cordyceps* lineage, consistent with Spatafora et al. 2007; *Diaporthe/Phomopsis;* and the Chaetothyriomycetidae). Endophytic life styles also arose from endolichenic ancestors, that is, fungi occurring in close associations with lichen photobionts in the context of living lichen thalli. These transitions occurred primarily in host-generalist lineages, including *Phoma,* some *Xylaria*, and various Hypocreales. Finally, transitions from saprotrophy to endophytism were observed in several cases, albeit relatively rarely; these were particularly common in Xylariaceae (see U'Ren et al. 2009).

By placing endophytic fungi in a phylogenetic context, we gain insights into the evolutionary trajectory of their associations, predictive power with regard to their functional traits, and testable hypotheses with which to structure analyses regarding host affiliations, genomic architecture, plant interactions, and life history strategies. Because such studies are based only on cultured endophytes to date, phylogenetic integration of next-generation/culture-free methods is greatly needed to understand whether additional functional groups of endophytes can be identified, based on their evolutionary history, how unculturable fungi will shift the relative frequency of evolutionary transitions across endophyte-containing lineages, and how the polyphyletic collection of fungal taxa that collectively share endophytic life styles can be partitioned for greater insight into their relationship with plant traits. For now, major challenges remain in integrating culture-free data sets into robust phylogenies, inferring function from data sets based on "barcode loci" alone (U'Ren et al. 2009), and categorizing the breadth of potential ecological modes even in cultured fungi (Arnold et al. 2009), thus calling for extensive study in the years to come.

6.5 CONCLUSIONS

As we begin to understand more about the evolutionary origins, ecological diversity, dispersal and infection mechanisms, and functional traits of endophytes in tropical forests, potential connections between theories developed for plant community ecology can be clarified to develop a clearer understanding of processes relevant to endophyte community assembly. In particular, we predict that trade-offs between growth and persistence in tropical woody plants result in plant traits that may influence endophyte abundances and community composition in predictable ways. Endophytes themselves may have similar trade-offs among growth and persistence strategies. Going forward, an empirical and trait-based approach focusing on fungal traits will be especially helpful for understanding the vast diversity of endophytes and their host relations (Aguilar-Triguernos et al. 2014; Krause et al. 2014). For this, we need a better understanding of fungal traits and fungal life histories *in planta*.

Although this chapter has focused primarily on the influences that plant traits have on fungi, it has given scant attention to the large literature showing that this is a bidirectional interaction—that is, that endophytic fungi can also influence plant traits. Evidence is mounting that endophytes, as well as bacterial symbionts and mycorrhizas, can alter their host traits and thus "shape" their own niche (see Rasmussen et al. 2008; Bever et al. 2010; Friesen et al. 2011; Mejía et al. 2014). Endophyte-induced traits can go beyond influencing the host defense mechanisms and may include the production of hormones and secondary metabolites that modify their host interactions with other trophic levels and responses to abiotic stress (Omacini et al. 2001; Rodriguez et al. 2009; Gao et al. 2011; Ding et al. 2012; Kivlin et al. 2013; Soliman and Raizada 2013). Much work remains to explore how diverse fungal endophytes influence the traits of their hosts in tropical forests and how these influences may shape not only plant gene expression, physiology, and ecology, but also long-term evolution. Given that host plant traits are well characterized and fungal endophytes show greater diversity than their host plants in a given area, it is likely that we will find predictable patterns of host traits influencing fungal endophytes, before we can make generalizations regarding the influence of diverse endophytes on their hosts.

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Author Query Sheet

Chapter No.: 6

Query No.	Queries	Response
AQ 1	Please check if the edit made to “a meta-analysis...processes” is OK.	
AQ 2	“Blonder et al. (2015)” has been changed to “Blonder et al. (2016)” as per the reference list. Please check.	
AQ 3	“Lüttge (2008)” has been changed to “Lüttge (2007)” as per the reference list. Please check.	
AQ 4	Please add “Veneklaas and Poorter (2006)” to reference list with complete details.	
AQ 5	Please add “Arnold (2008)” to reference list with complete details.	
AQ 6	This term has been abbreviated above (at the first occurrence). Would you like to retain the full form here or delete the full form and retain only the abbreviation?	
AQ 7	Please check if a word is missing between “increase” and “in.”	
AQ 8	The meaning of the sentence “This...diseases” is unclear. Please check and revise.	
AQ 9	Please add “Coley and Aide (1995)” to reference list with complete details.	
AQ 10	Please check if the edit made to “Connections...time” is OK.	
AQ 11	“Wei et al. (2015)” has been changed to “Wei et al. (2016)” as per the reference list. Please check.	
AQ 12	Please consider providing editor name and publisher location for “Allen et al. (1991).”	
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AQ 39	Please update the complete details (if any) for “Wei et al. (2016).”	
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