Tree Endophytes: Cryptic Drivers of Tropical Forest Diversity

Eric A. Griffin and Walter P. Carson

Abstract Roots and leaves comprise two of the largest microbial habitats on Earth, particularly in tropical forests where root and leaf surface areas are extremely high and microbes are abundant and diverse. Fungal and bacterial endophytes are primarily acquired via contagious spread from the surrounding environment. The soil is an important reservoir for both fungal and bacterial endophytes; we term this a *soil microbial bank* and suggest that it functions similarly to a soil seed bank. Because most ($\sim$75%) studies have found a strong positive relationship between plant diversity and soil microbial diversity, we predict that as plant diversity increases so will endophyte taxonomic and functional diversity. Once inside plant host tissues, endophytes can act as mutualists and increase plant performance directly by producing plant hormones, or indirectly by decreasing fungal or insect damage by up to 80%. Recent studies, however, have demonstrated that there are costs associated with hosting "beneficial" endophytes for tropical trees. This is important because it challenges more traditional dichotomies (e.g., beneficial or deleterious) about endophytes and suggests that there are highly complex and context-dependent trade-offs and costs involved in plant-endophyte interactions. Though they comprise a cryptic component of tropical forests, plant-microbe interactions may typically regulate tree diversity, composition, and forest function at neighborhood and even regional scales. For example, pathogens may maintain tree diversity by reducing the fitness of common species in areas where plant host density is high or where hosts are close to reproductive conspecific adults. Moreover, plant-endophyte interactions, whether pathogenic or mutualistic, may comprise an entirely novel dimension of niche differentiation for coexisting tree species. Overall, tree endophytes in tropical forests are complex, yet critical drivers of forest dynamics and function.

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1 Introduction

Together, plant roots and leaves comprise two of the world's largest microbial habitats, yet we know little about the microbes that occur in these habitats, particularly in tropical forests (Curl and Truelove 2012; Griffin and Carson 2015). Indeed, the global root area is over 100 million km^2 and the global leaf area is over 1 billion km^2, which alone is more than double the earth's land surface area (Jackson et al. 1997; Vorholt 2012). Moreover, microbial endophytes have been isolated from *every* plant species studied to date, which includes species from tundra to deserts, agricultural systems, and tropical rainforests (Stone et al. 2000; Strobel et al. 2004; Rodriguez et al. 2009; Aly et al. 2010; Strobel 2012). The ubiquitous distribution of endophytes and their high diversity and abundance in some biomes suggest that these cryptic organisms can be powerful drivers of ecological processes. Indeed, studies have demonstrated that fungal and bacterial endophytes can increase or decrease plant performance, regulate plant diversity, and cause cascading effects up and down trophic levels (e.g., Clay and Holah 1999; Griffin et al. 2016, 2017; Laforest-Lapointe et al. 2017; reviewed by Rodriguez et al. 2009; Saikkonen et al. 2010; Griffin and Carson 2015; Hardoim et al. 2015; Brader et al. 2017). Studies to date, however, have focused primarily on grasses and agricultural crops but not trees, which store the bulk of above-ground carbon worldwide (Rudgers and Clay 2007; Hyde and Soytong 2008; Aly et al. 2010; Porras-Alfaro and Bayman 2011; but cf Zimmerman and Vitousek 2012; Griffin et al. 2016, 2017; Laforest-Lapointe et al. 2017).

In this book chapter, we review what is known about the identities, diversity, ecological origins, and impacts of bacterial and fungal endophytes on tropical tree hosts and their resident plant communities. In particular sections of this chapter where studies are numerous and bacteria and fungi are distinguishably different, we write separate sections on bacteria and fungi; otherwise, in other sections we group bacteria and fungi together. We define *endophytes* as bacteria or fungi that have colonized the interior portions of plant tissues (De Bary 1866; Henis and Bashan 1986; Hardoim et al. 2015; Griffin and Carson 2015). We define the *endosphere* as the interior portion of any plant tissue from seed to adult (Compant et al. 2010). We define *operational taxonomic units* (OTUs) as sequences delineated by percent DNA sequence similarity (typically 97%).

Because most endophyte studies have focused on graminoids and other herbaceous species, we use these to draw some general inferences about the identities and impacts of endophytes among tropical trees. It is important to note, however, that grass endophytes are different from tree endophytes in two major ways. First, grass endophytes are more likely to be vertically transmitted from mother to offspring via seed whereas in trees, endophytes typically accumulate horizontally via contagious spread (Arnold 2007; Rodriguez et al. 2009; Hardoim et al. 2015; Christian et al. 2017a). However, this conclusion remains tenuous because the degree to which tree *bacterial* endophytes are vertically or horizontally transmitted is poorly known and awaits further research (Griffin and Carson 2015; Hardoim et al. 2015; Brader et al.

2017; Frank et al. 2017; but cf Edwards et al. 2015 for horizontal transmission in rice). Moreover, grass endophytes are distantly related to tree-associated endophytes (reviewed by Rodriguez et al. 2009), which alone warrants further research. For one, phylogenetic differences among grass- and tree-associated endophytes are artifacts of host life form differences or due to geographic isolation of sites and microbial dispersal limitation. We argue that the latter might actually be more important and hypothesize that the degree of phylogenetic overlap and endophyte community similarity will increase substantially in communities where grasses are relatively depauperate and immersed within habitats dominated by woody species (e.g., forests). Nevertheless, applying any conclusions from grasses to trees has limitations.

In this chapter, our main goals are the following:

1. Define microbial endophytes and discuss endophyte taxonomy with a focus on the tropical biome (Sect. 2.).
2. Consider the ecological origins of microbial endophytes (Sect. 3.) and how they colonize the endosphere (Sect. 4.), with a particular focus on tropical endophytes.
3. Synthesize the impacts of endophytes on host performance (Sect. 5.) and discuss the potential large-scale implications of plant-microbe interactions (Sect. 6.).

Ultimately, we argue that though they comprise a cryptic component of tropical forests, endophytes are critical in regulating tree diversity, composition and forest function.

2 What are Endophytes?

Though German botanist Heinrich Friedrich Link was the first to describe endophytes in 1809, De Bary (1866) first defined “endophyte” as “any organism occurring within plant tissues.” Since then, however, many definitions for “endophyte” have been used (reviewed by Schulz and Coyne 2006; Griffin and Carson 2015; Hardoim et al. 2015). In fact, multiple definitions of the word “endophyte” are likely used among chapters in this book. In the last 25 years, the most commonly used definition is from Petrini (1991), who defined endophytes as “all organisms inhabiting plant organs that at some time in their life, can colonize internal plant tissues *without causing apparent harm to the host*.” We point out two serious problems with this definition. First, microbes reside along a “continuum of infection patterns” (Wilson 1995) whereby a microbe can function as a mutualist, pathogen, or commensal depending on the virulence of the microbe, host defense responses, and environmental conditions (e.g., water availability, light availability, etc.; Johnson et al. 1997; Saikkonen et al. 1998; Schulz and Boyle 2005; Kogel et al. 2006; Johnson and Graham 2013; Mandyam et al. 2014). Thus, under

Petrini's definition, some endophytes would be defined as beneficial or benign when in fact they can become pathogenic (Schulz and Coyne 2006). Moreover, endophytic pathogens can reside within plant tissues but show no signs of infection, yet these microbes can still cause significant decreases in host performance (e.g., Bashan and Okon 1981; Newsham et al. 1994; Malcolm et al. 2013). Bashan and Okon (1981) provided a striking demonstration of this when they found that tomato plants grown in soil inoculated with the pathogen *Pseudomonas syringae* (Gammaproteobacteria) were morphologically symptomless but produced 30% less foliage than plants in sterile soil. Thus, defining endophytes strictly as beneficial or benign and thereby excluding pathogens from this definition is no longer tenable. The second problem with categorizing endophytes by function is that culture-based methods, which retrieve as little as 0.1–10% of entire microbial communities, and subsequent inoculation experiments of particular strains must be performed to assess microbial functionality (Amman et al. 1995). Thus, using a functionally-based definition of endophyte (e.g., not pathogenic) may be unwise because currently it is virtually impossible to characterize the functionality of the large majority of endophytes. For these reasons, we feel that the most parsimonious definition provided by De Bary (1866) is best; specifically, an endophyte is any microbe that occurs within plant tissue (Henis and Bashan 1986; Hardoim et al. 2015; Griffin and Carson 2015; Christian et al. 2017a).

Currently, the total number of identified plant fungal endophyte sequences outnumbers bacterial endophytes. To date, over 8,000 fungal endophytes have been identified and placed within 4 phyla, Ascomycota (31%), Basidiomycota (20%), Glomeromycota (40%), and Zygomycota (0.06%; almost 9% are unidentified; see Table 2 in Hardoim et al. 2015). Fungal endophytes have been placed within 20 classes, 39% are Glomeromycetes (Glomeromycota), 19% are Agaricomycetes (Basidiomycota), and 15 and 9% are in Dothideomycetes and Sordariomycetes, respectively (Ascomycota). Comparatively, over 7,000 bacterial endophytes have been identified in 23 phyla, 21 in the Bacterial Kingdom (99% of all sequences) and 2 in Archaea (1%). Eighty-one percent of all bacterial endophytes lie within 3 phyla, Actinobacteria (20%), Firmicutes (17%), and Proteobacteria (44%; see Table 1 in Hardoim et al. 2015). How broadly these relative percentages apply is unclear because endophytes have been primarily studied among temperate crop species and have only been characterized in a few wild gymnosperms and angiosperms (see reviews from Arnold 2007; Arnold 2008; Berg 2009; Rodriguez et al. 2009; Compant et al. 2010; Hardoim et al. 2015; Brader et al. 2017). Clearly, fungal and bacterial endophytes are diverse, yet even basic surveys of their distribution and abundance among tropical trees remain to be done.

2.1 Tree Endophytes in Tropical Forests

While it is likely that microbial endophytes are more diverse in tropical forests than temperate forests, most studies to date have used culture-dependent techniques to characterize endophyte communities among plant species. Arnold and Lutzoni (2007) demonstrated that among 22 plant species (14 tree species, 4 shrubs, 2 mosses, 1 fern and 1 liverwort), culturable fungal endophyte diversity was 24% higher among tropical than among their temperate hosts. Moreover, latitude explained almost 75% of the variation in the ratio of endophyte-infected leaves. Specifically, endophytes were isolated from 97–100% of leaves in a tropical forest in Panama compared to only 1% for the arctic site (Fig. 1). However, other culture-based studies of fungal endophyte communities reveal that fungal endophyte communities are not always highly diverse in tropical forests (e.g., Cannon and Simmons 2002; Suryanarayanan et al. 2002, 2003, 2011; Murali et al. 2006). For example, Suryanarayanan et al. (2003) found that that fungal leaf endophyte

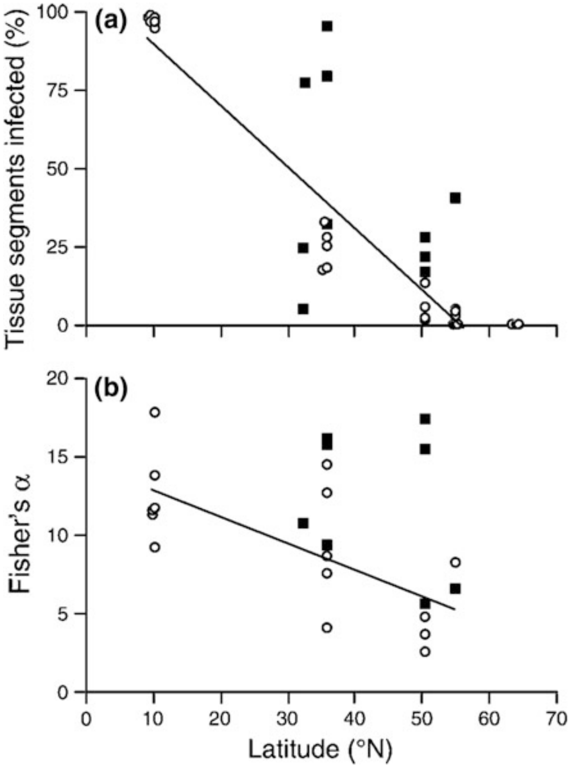

Fig. 1 **a** Latitudinal gradient of endophyte infections (from Arnold and Lutzoni 2007). The percentage of tissue fragments (each 2 mm^2) infected by culturable endophytes for 34 host species/site combinations, representing eight localities ranging from lowland tropical forest (Barro Colorado Island (BCI), Panama) to arctic tundra (near Iqaluit, Nunavut, Canada). Solid squares indicate conifers; open circles indicate all other hosts. **b** Latitudinal gradient of endophyte diversity. Fisher's alpha for 23 host–site combinations, representing 1202 strains of endophytic fungi from six localities ranging from tropical forest at BCI to northern boreal forest (Schefferville, Quebec, Canada). Solid squares indicate conifers; open circles indicate all other hosts

diversity among 11 tree species in a tropical forest in India was 22% lower (Fisher's alpha diversity = 9.89) compared to Arnold and Lutzoni's findings among trees in Panama (Fisher's alpha = 12.65, Arnold and Lutzoni 2007). Currently, it is difficult to say anything definitive about patterns of endophyte diversity among tropical forests because of the paucity of studies and the reliance on culture-based methods.

2.1.1 Bacterial Endophytes

In the first study of foliar bacterial endophyte communities among tropical forest trees (however see Gayathri et al. 2010 and Castro et al. 2014 for mangrove trees), Griffin (2016) identified a total of more than 5200 (non-singleton) OTUs among *seedlings* of only five tree species, with a mean of almost 300 OTUs per individual seedling. Overall, 92% of endophytes were found within Actinobacteria (49%), Proteobacteria (32%) and Firmicutes (11%). Thus, Actinobacteria were disproportionately represented compared to bacteria found in other plant species (20%; Table 1 in Hardoim et al. 2015). The high diversity of Actinobacteria is noteworthy because these bacteria produce almost half of the world's antimicrobial compounds (Berdy 2005; Waksman et al. 2010; Berdy 2012; see "Pathogen Protection" below). Clearly, more studies using culture-independent techniques are needed to better understand the identities and functions of endophyte communities among host species in tropical forests.

2.1.2 Fungal Endophytes

To our knowledge, Zimmerman and Vitousek (2012) conducted the first culture-independent sequencing of the foliar endophytic community of *Metrosideros polymorpha* (Myrtaceae), an evergreen tropical tree endemic to large islands in Hawaii. They identified a total of 2500 (non-singleton) OTUs and a mean of 341 OTUs per tree among seven sites that spanned 80 km. Overall, differences in annual precipitation (from <500 to >5,000 mm/y), elevation (100–2,400 m), and substrate (lava-flow) age (100–3,500 yr) explained over half of endophyte diversity and community composition ($P < 0.01$; $R^2 = 0.56$). These findings are important because they show that endophyte communities vary drastically within a single species, over relatively short distances, and are sensitive to key substrate, resource, and elevational gradients.

Overall, Zimmerman and Vitousek (2012) identified a disproportionately large portion of sequences in Ascomycota (85%) compared to those identified to date in all other plants (~31%; Table 2 in Hardoim et al. 2015). Specifically, 73% of the Ascomycota sequences were in the class Dothideomycetes, the largest Ascomycota class and one that contains at least 18 plant pathogens (Ohm et al. 2012). Other phyla represented included Basidiomycota (0.8%) and Streptophyta (0.6%). A large percentage (40%) of the sequences, however, could not be identified in the Genbank sequence database.

3 What Structures Endophyte Communities?

3.1 Vertical Transmission: Common in Herbs But Not Trees

Despite the critical ecological importance of endophytes, we do not know whether the majority of tree-associated microbes, particularly bacteria, are transmitted from mother to offspring (i.e., vertical transmission) or via contagious spread (i.e., horizontal transmission). On one hand, microbes may be transmitted vertically via seed infections and ultimately colonize reproductive tissues after germination and transmit microbes from one generation to the next (reviewed by Griffin and Carson 2015; Truyens et al. 2015). For example, clavicipitaceous fungi (see Box 1) are a fungal class whose fungi associate with grasses as obligate symbionts, where they establish long-term associations and colonize systemically among all host tissues (reviewed by Kuldau and Bacon 2008). Moreover, these fungi are primarily vertically transmitted from mother to offspring via seed (Clay 1989; Rodriguez et al. 2009). Saikkonen et al. (2004) proposed that vertical transmission often occurs in grasses because their smaller stature and less complex architecture (relative to trees) allow for endophytes to rapidly spread throughout the plant, including reproductive tissues. Nonclavicipitaceous fungi associated with tree hosts, however, are primarily horizontally transmitted and infect host tissues more locally (Arnold 2005; Ganley and Newcome 2006; Arnold 2007; Arnold 2008; Rodriguez et al. 2009; Saikkonen et al. 2010; Sanchez-Marquez et al. 2012; Hodgson et al. 2014; Christian et al. 2015). Indeed, results to date suggest that tree endophytes do not commonly colonize seeds vertically from the mother plant. For example, Ganley and Newcombe (2006) found that only 16 of 800 seeds (2%) of *Pinus monticola*, a species native to the western U.S., contained fungal endophytes. In addition, Zalamea et al. (2015) recently demonstrated that only 0–4% of fresh seeds from 4 tropical tree species native to Panama were infected with bacteria and only 2–10% were infected with fungi. The identities of fungal and bacterial isolates were not characterized. Because of such low seed infection ratios, it appears that vertical transmission of endophytes is far less common than horizontal transmission. Though numerous studies have demonstrated that tropical tree endophytes provide many benefits to plant hosts, pathogenic fungi are particularly prominent and destructive in tropical forests (see “The impacts of microbial endophytes on plant hosts” and “Pathogens” sections below). Moreover, Mejia et al. (2014) recently demonstrated clear costs associated with hosting *beneficial* endophytes for the tropical tree *Theobroma cacao* (Malvaceae); these included decreased nitrogen metabolism and a substantial reduction in photosynthesis (33%). This finding, if common, is important because endophytes that provide some benefit to their hosts may typically come at a cost in terms of plant metabolism. Thus, the degree of benefit of the endophyte may vary strongly with host condition and resource availability, making it even more difficult to identify endophytes as beneficial or harmful because of a high degree of context-dependency.

Box 1. Classification of Endophytic Fungi

Rodriguez et al. (2009) divided fungal endophytes into different classes based upon the method and location of host colonization. Class I, the clavicipitaceous fungi (Hypocreales; Ascomycota), are those associated with grasses and are primarily vertically transmitted from mother to offspring via seed. Class II endophytes are classified in the Dikarya subkingdom and are primarily in the two divisions Ascomycota or Basidiomycota. Class II endophytes colonize roots and leaves via seed coats and rhizomes and may be either vertically or horizontally transmitted. Class III endophytes are also almost exclusively classified in Ascomycota or Basidiomycota and are those primarily found among trees. Moreover, Class III endophytes colonize above-ground plant tissues via horizontal transmission and have high diversity compared to all other classes. Finally, Class IV endophytes are dark, septate endophytes and restricted to roots, where they reside inter- or intra-cellularly in the cortical cell layers. Here, we primarily focus on Class III endophytes because these are the tree-associated endophytes and are particularly common in tropical forests (e.g., Lodge et al. 1996; Frohlich and Hyde 1999; Arnold et al. 2000; Gamboa and Bayman 2001; Arnold and Herre 2003; Arnold et al. 2003; Gamboa et al. 2003; Arnold and Lutzoni 2007; Higgins et al. 2007; Arnold 2008; Zimmerman and Vitousek 2012).

3.2 Horizontal Transmission

3.2.1 Endophyte Colonization of Roots

Soil is a key reservoir for microbial endophytes in tropical forests and represents a soil microbial bank similar to a soil seed bank. A single gram of soil can host up to 10,000 fungal cells and hundreds of fungal species (Buee et al. 2009; Fierer et al. 2007a; Rousk et al. 2010). Comparatively, a gram of soil hosts up to one billion bacterial cells and thousands of bacterial species (Whitman et al. 1998; Torsvik et al. 2002; Gans et al. 2005; Schloss and Handelsman 2006; Fierer et al. 2007a, b; Rousk et al. 2010). Moreover, viable microbial cells may persist for decades or even longer in soil where at any time 50–80% of microbial cells are dormant (reviewed by Lennon and Jones 2011). Thus, soil microbes may commonly use a bet-hedging strategy where they do not colonize plant hosts until environmental conditions are favorable.

Bacteria and fungi can colonize seeds in the soil before germination or be mechanically chauffeured from the soil onto the developing seedling during germination (reviewed by Griffin and Carson 2015; Llado et al. 2017). For example, Zalamea et al. (2015) found that prior to germination, fungal infection of the interior of surface-sterilized seeds increased from ~4–15% and bacterial infection increased from ~2–50% after only a single month in situ in a tropical forest in Panama. Thus, it appears that the soil microbial bank is likely critical to understanding seed and seedling colonization.

The roots of seedlings, saplings, and adults produce root exudates composed of carbohydrates, amino acids, and organic acids that recruit fungal and microbial endophytes (Phillips et al. 2011; Wang et al. 2016). In fact, up to 40% of newly photosynthesized C among non-legume temperate crops and trees can be in the form of root exudates which function to recruit mycorrhizal fungi and nitrogen-fixing bacteria (reviewed by Kuzyakov and Domanski 2000; Werth and Kuzyakov 2010). This is likely a major cost to plants and suggests just how critical these endophytes are for plant hosts.

3.2.2 The Plant Diversity-Soil Organic Heterogeneity Hypothesis

Though the impacts of plant diversity on ecosystem function and trophic interactions are well documented (recent reviews by Tilman et al. 2014; Lefcheck et al. 2015; Oliver et al. 2015; Schleuning et al. 2015; Tilman 2016; Duffy et al. 2017), to our knowledge the degree to which plant diversity structures endophyte communities has never been considered. Hooper et al. (2000) and Waldrop et al. (2006) proposed that increased plant diversity increases the range of organic substrates entering the soil, thus creating more niche space that can accommodate a greater diversity of soil microbes. We term this the *plant diversity-soil organic heterogeneity hypothesis* to distinguish this from other plant diversity hypotheses. Indeed, 72% of observational or experimental studies have demonstrated a positive relationship between plant diversity and soil microbial diversity, and this result is consistent with free-living soil microbes, root-associated microbes (e.g., AM and EM fungi), and phyllosphere bacteria (Table 1). However, most of these studies (over 70%) have been conducted in grasslands, agricultural fields, or in the greenhouse. Only 7 studies (14%) were conducted in tropical forests, where all but one (Schappe et al. 2017) showed a positive relationship between plant diversity and soil microbial diversity. To our knowledge, the relationship between plant diversity and bacterial endophytes has never been evaluated. Still, it is likely that the soils of hyper-diverse tropical forests host more diverse pools of microbes and these soils are a major reservoir of plant endophytes (but cf Fierer and Jackson 2006).

3.2.3 Endophyte Colonization of Seedlings

Endophytes primarily colonize tropical tree seedlings via contagious spread (e.g., horizontal transmission; Arnold and Lutzoni 2007) and gain access to the leaf interior via a few key mechanisms. Indeed, as many as 36,000 fungal spores per day colonize endophyte-free tropical tree seedlings transplanted into the field (Arnold and Herre 2003; Gilbert and Reynolds 2005). The sources of these spores remain

Table 1 Summary of studies which demonstrate (empirically or observationally) the impacts of above-ground plant diversity on below-ground microbes

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Grassland	AM	Transplant experiment with *Lespedeza capitata*, *Schizachyrium scoparium*, and *Liatris aspera* in 1, 7, 15 species plots with native grass species at Cedar reek, Minnesota, USA	Exp	Increased plant diversity increased AM diversity for *L. capitata* but not *S. scoparium* or *L. aspera*	Burrows and Pfleger (2002a)
Grassland	AM	1, 2, 8, or 16 species mixtures (Grasses and herbs) at Cedar Creek, Minnesota, USA	Exp	16-species plots increased AM spore abundance by 30–150% and volume by 40–70% compared to 1-sp plots	Burrows and Pfleger (2002b)
Grassland	AM	*Carex flacca*, *Festuca ovina* transplant experiment in Derbyshire, UK	Exp	12-species plots increased *F. ovina* AM diversity by 100% but had no effect on *C. flacca* AM diversity	Johnson et al. (2003)
Grassland	AM	137 plant species and 18 AM species in Wisconsin, USA	Obs	Plant species richness positively correlated with AM species richness	Landis et al. (2004)
Grassland	AM	Fields of either 27 or 43 plant species in Thuringia, Germany	Obs	Plant diversity alters AM composition but not diversity	Borstler et al. (2006)
Grassland	AM, soil fungi, bacteria	1, 4, 8, 14 species mixtures from 16-species pool of 4 C4 grasses, four C3 grasses, 4 legumes, and 4 forbs at Cedar Creek, Minnesota, USA	Exp	Increasing plant richness increased microbial biomass, fungal abundance, and AM abundance	Chung et al. (2007)
Grassland	AM	Plots with 1, 2, 4, 8, 16, and 60 species mixtures (Grasses and herbs) in Jena, Germany	Exp	Plant richness increased AM richness but not diversity	Konig et al. (2010)
Grassland	AM	1 or 16 species plots at Cedar Creek, Minnesota, USA	Exp	Plant richness was negatively correlated with AM richness	Antoninka et al. (2011)

(continued)

Table 1 (continued)

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Grassland	AM	Mixed grass prairie with 75 vascular species, Saskatchewan, Canada	Obs	Plant species richness was positively corrected with AM richness	Hiiesalu et al. (2014)
Grassland	AM	47 grass and herb species; focal species *Festuca brevipila* in Germany	Obs	No significant effect of plant neighbors on AM community	Horn et al. (2017)
Grassland	Soil bacteria	Grasslands dominated by *Lolium perenne* L., the legume *Trifolium repens* L., and *Poa annua* L. in Waikato, New Zealand	Exp	No effects of plant diversity on soil microbial communities	Wardle et al. (1999)
Grassland	Soil bacteria	32 grassland communities in Lupsingen, Switzerland	Exp	Increased plant diversity increased soil microbial diversity	Stephan et al. (2000)
Grassland	Soil bacteria	Low diversity (2 grasses, 1 legume, 1 forb) and high diversity plots (5 grasses, 5 legumes, 5 forbs) in Veluwe, Netherlands	Exp	Increased plant diversity increased soil bacterial diversity	Kowalchuk et al. (2002)
Grassland	Soil bacteria and fungi	Richness (1 or 2) of combinations of 6 grass species in Kansas, USA	Exp	No effects of plant richness on bacterial or fungal communities	Porazinska et al. (2003)
Grassland	Soil bacteria	Species combinations among 9 grass, forb, and legume species in New Zealand	Exp	Plant composition but not diversity impacted soil microbial diversity	Wardle et al. (2003)
Grassland	Soil bacteria	1, 2, 4, 8, or 16-sp plots from pool of 18 grasses, legumes, forbs, and trees at Cedar Creek, Minnesota, USA	Exp	Increased plant diversity increased soil microbial diversity and biomass	Zak et al. (2003)
Grassland	Soil bacteria	Monoculture (*Cordia alliodora*), 3-species (*C. alliodora*, *Heliconia imbricate*, *Euterpe oleracea*), 5 species (*C. alliodora*, *Hyeronima alchorneoides*, *Cedrela odorata*, *Euterpe macrospadix*, *E. oleracea*) in Costa Rica	Exp	No effects of plant diversity on soil microbial community	Carney et al. (2004)

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Table 1 (continued)

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Grassland	Soil bacteria	1, 2, 3, or 4 species plots; *Festuca rubra* L., *Holcus lanatus* L., *Achillea millefoilum*, *Rumex acetosa* L. in Nemours-Saint-Pierre, France	Exp	Increasing plant diversity increased soil microbial diversity	Loranger-Merciris et al. (2006)
Grassland	Soil bacteria	1, 2, 3, 4, 8, 16, 60 species plots with native grassland species in Thuringia, Germany	Exp	Plant diversity increased soil microbial diversity	Eisenhauer et al. (2011)
Grassland	Soil bacteria	1, 4, and 9 species plots from pool of 16 herbaceous species in Jena Germany	Exp	Increased plant diversity increased microbial richness	Eisenhauer et al. (2013)
Grassland	Soil bacteria, fungi	1, 2, 4, 8, 16, or 60 species mixtures of perennial grasses in Jena, Germany	Exp	Plant functional and phylogenetic diversity increased soil bacterial and fungal diversity	Milcu et al. (2013)
Grassland	Soil bacteria	Grassland species across diversity gradients (globally)	Exp	Plant richness increased Beta but not alpha soil bacterial diversity	Prober et al. (2015)
Grassland	Soil bacteria	1, 2, 4, 8, 16, and 60 species plots selected from a pool of 60 grassland species in Jena, Germany	Exp	Increased plant richness (and genetic diversity) increased soil microbial diversity	Lange et al. (2015)
Grassland	Soil bacteria	*Andropogan gerardii*, *Schizachyrium scoparium*, *Lespedeza capitata*, *Lupinus perennis* grown in 1, 2, 4, 8, and 16 species mixtures in Cedar Creek, Minnesota, USA	Exp	Plant richness decreased soil microbial diversity	Schlatter et al. (2015)
Grassland	Soil fungi	Forbs, sedges, grasses, and legumes across 50 sites in China	Obs	Increasing plant richness correlated with increased soil fungal richness	Yang et al. (2017)
Grassland	Rhizo-sphere bacteria	Dominated by 7 grass species in Fasset Hill, UK	Obs	Plant community composition correlated with different rhizosphere communities (diversity not measured)	Nunan et al. (2005)

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Table 1 (continued)

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Temperate forests	EM	*Abies balsamea*, *Picea glauca*, *Betula papyrifera*, *Pinus banksiana*, *Populus tremuluoides*, *Populus balsamifera* in Quebec, Canada	Obs	Sites with higher tree diversity correlated with higher EM diversity	Kernaghan et al. (2003)
Temperate forests	EM	Soil samples from forest transects in Iran		Plant community diversity correlated with EM diversity	Bahram et al. (2012)
Temperate forests	EM, soil fungi	2, 3, 5 species of *Pinus sylvetsris*, *Picea abies*, *Larix sibirica*, *Betula pendula*, *Alnus glutinosa* in Finland; natural regeneration in Estonia	Exp	Tree diversity increased EM diversity in Finland and increased soil fungal diversity in Estonia	Tedersoo et al. (2016)
Temperate and subtropical forests	Soil fungi	Subtropical evergreen forests in China	Obs	Plant diversity positively correlated to soil fungal diversity to a greater degree in subtropical forests compared to deciduous forests	He et al. (2017)
Temperate forests	EM, soil fungi	Estonian forests dominated by *Pinus sylvestris* L.	Obs	Plant species richness increased fungal diversity, particularly EM	Hiiesalu et al. (2017)
Temperate forest	Leaf bacteria	1, 2, 4, 12 species plots from a pool of 19 tree species in Quebec, Canada	Exp	Functional tree diversity and richness increased leaf-bacterial diversity	Laforest-Lapointe et al. (2017)
Temperate forest	AM	47 herb, shrub, and tree species in Iran	Obs	Increased diversity was positively correlated with AM diversity	Mirzaei and Moradi (2017)
Tropical forest	EM	Mixed dipterocaro forest in Sarawak, Borneo	Obs	Though not explicitly tested, data suggest that alpha, beta, and phylogenetic diversity of plants impact EM diversity	Peay et al. (2010)

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Table 1 (continued)

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Subtropical evergreen forest	EM	159 tree species in China	Obs	Plant diversity increased EM diversity by ~15–~50%	Gao et al. (2013)
Tropical forests	Soil fungi	Western Amazonia basin, Peru	Obs	Soil fungal richness increased with increased tree species richness	Peay et al. (2013)
Tropical forest	Soil fungi	Monoculture and polyculture plots using *Hyeronima alchorneoides*, *Pentaclethra macrobloba*, *Virola koschnyi*, *Vochysia guatemalensis* in La Selva, Costa Rica	Exp	Tree community caused differences in soil fungal abundance, richness, and composition	Kivlin and Hawkes (2016b)
Tropical forest	Soil fungi	159 plant species, in ridge and valley in China	Obs	Plant species richness positively correlated with soil fungal richness in ridge habitats but not in valley habitats	Gao et al. (2017)
Tropical forests	Soil fungi, AM	3 forest sites in Panama with differing levels of tree diversity	Obs	Increased plant diversity was correlated with non-AM diversity but not AM diversity	Schappe et al. (2017)
Tropical forest	Soil bacteria	Monoculture and polyculture plots using *Hyeronima alchorneoides*, *Pentaclethra macrobloba*, *Virola koschnyi*, *Vochysia guatemalensis* in La Selva, Costa Rica	Exp	Tree community caused differences in soil bacterial abundance, richness, and composition	Kivlin and Hawkes (2016a)
Greenhouse	AM	*Nassella pulchra*, *Avena barbata*, *Bromus hordeaceous*, *Vulpia microstachys* (grassland species), California, USA	Exp	Plant neighbors alter AM communities (diversity not measured)	Hausmann and Hawkes (2009)
Greenhouse	AM	1, 2, and 4 species plots from pool of five native and five exotic congeners in Texas, USA	Exp	Plant richness caused changes in AM composition (diversity not measured)	Kivlin and Hawkes (2011)

(continued)

Table 1 (continued)

System	Soil taxa	Species/treatments	Obs or Exp	Impact of plant diversity on microbial diversity	Study
Greenhouse	Soil bacteria	14 grassland species, Cedar Creek, Minnesota, USA	Exp	Plant richness increased soil microbial diversity	Antoninka et al. (2009)
Greenhouse	Soil bacteria, fungi	1, 3, 6, 12 species in mesocosms from a pool of 12 grassland species in Ithaca, New York	Exp	Plant diversity increased soil bacterial and fungal diversity	Thompson and Kao-Kniffin (2016)
Agricultural fields	AM	Weed communities among citrus orchards in Zhejiang Province, China	Exp	AM spore abundance increased with plant species richness	Chen et al. (2004)
Agricultural fields	AM	*Zea mays* monoculture or *Z. mays* and *Crotalaria grahamiana* mixtures in western Kenya	Exp	Polyculture fields changed AM composition but not diversity compared to *Z. mays* monoculture	Mathimaran et al. (2007)
Agricultural fields	AM, soil fungi, bacteria	Monocultures to rotations of corn, soybean, red clover, rye clover, wheat in Michigan, USA	Exp	Increasing crop rotation increased soil bacteria, non-AM fungi but decreased AM fungi	Tiemann et al. (2015)
Agricultural fields	Soil bacteria	Fields with different land-use histories (e.g., grassland, agricultural rotation, arable land, maize, etc.) in Bennekom, Netherlands	Obs	Increases in plant diversity positively correlated with soil microbial diversity	Garbeva et al. (2006)
Shrub land	AM	Shrub, forb, and graminoid species in Cordoba, Argentina	Exp	Removal of species caused no difference in AM abundance or evenness	Urcelay et al. (2009)
Meta-analysis of 26 publications 50.	AM	52 plant grass and tree species across tropical forests, grasslands, temperate forests, abandoned agricultural sites	Obs	Hyper-diverse tropical forests had >250% higher AM richness than abandoned agr sites and >125% higher richness than grasslands and temperate forests	Opik et al. (2006)

We include studies of free-living soil bacteria and fungi, as well as root-associated bacteria and fungi (e.g., arbuscular mycorrhizae (AM), ectomycorrhizal fungi (EM), or rhizosphere bacteria). Overall, 70% of studies were conducted in grasslands, agricultural fields, or in the greenhouse, while 14% of studies were conducted in tropical forests, 14% in temperate forests. We found that 72% of observational or experimental studies have demonstrated a positive relationship between plant diversity and soil microbial diversity, and this result is consistent with free-living soil microbes, root-associated microbes (e.g., AM and EM fungi), and phyllosphere bacteria poorly understood and we have no data regarding the rates of bacterial colonization; however, this may well exceed rates of fungal colonization. Water and animal vectors (particularly insects) spread fungi and bacteria among tropical trees (reviewed by Griffin and Carson 2015). For example, wind and rain caused by hurricanes are the primary mechanisms for dispersal of *Xanthomonas axonopodis* (Gammaproteobacteria), the bacterial pathogen that colonizes leaves and causes citrus canker disease (Gottwald et al. 2002; Graham et al. 2004; Irey et al. 2006). In fact, *X. axonopodis* dispersed at least 50 km, and likely much further, to cause new outbreaks citrus canker following a hurricane in Florida (Irey et al. 2006; Gottwald and Irey 2007). Finally, insect vectors in tropical forests, which are orders of magnitudes more abundant and diverse compared to temperate systems, may disperse endophytes at small scales among plant hosts or potentially up to thousands of miles via migration (May 1988, 1990; Brown and Hovmoller 2002; Hamilton et al. 2010; Chapman et al. 2015; Stork et al. 2015). Indeed, 24 different xylem-feeding insect species (Hemiptera) vector (in their foregut) the bacterium *Xylella fastidiosa* (Gammaproteobacteria), which causes disease among temperate and tropical tree species (Purcell et al. 1979; Krugner et al. 2000; Redak et al. 2004; Azevedo et al. 2016; Lopes et al. 2016). One of the diseases caused by *Xylella fastidiosa* is citrus variegated chlorosis (CVC), which causes $120 million in losses per year in Latin American (Bove and Ayres 2007; Lopes et al. 2016). Moreover, larger insects, particularly in the orders Orthoptera and Lepidoptera, undertake seasonal movements of more than a thousand miles (reviewed by Chapman et al. 2015). It is likely that these insects spread bacteria and fungi among plant species during these migrations, but data are non-existent.

4 Reaching the Endosphere

4.1 Bacteria

Bacterial endophytes may colonize root and leaf tissue, where they can then act as mutualists or pathogens. As stated above, trees may recruit beneficial bacterial endophytes by producing root exudates, though both beneficial and pathogenic bacteria colonize root interiors via cracks in lateral root junctions, wounds, and root hairs (Sorensen and Sessitsch 2007; Hardoim et al. 2008; Mercado-Blanco and Prieto 2012). For example, rhizobial bacteria, which are more abundant in tropical soils compared to temperate soils, use a complex system of signal exchanges with plant hosts to enter roots via hairs or lateral root cracks (Hedin et al. 2009; Gourion et al. 2015; Pajares and Bohannan 2016). Similarly, bacteria on the leaf surface enter leaves at leaf openings such as trichome bases, stomata, or wounds created by insects (Beattie and Lindow 1995; Agrios 2005; reviewed by Griffin and Carson 2015). Pathogenic bacteria in particular gain access to leaf interiors with sophisticated and highly evolved secretion systems to bypass or suppress plant immunity (see “Pathogens” section). For example, *P. syringae* (Gammaproteobacteria), the most well-studied plant pathogen in the world, produces coronatine and syringolin to suppress host immunity to pathogens and induces stomatal opening, enabling bacteria to access the apoplast (Zhao et al. 2003; Melotto et al. 2006, 2008; Schellenberg et al. 2010). Because bacterial pathogens typically have secretion systems that deliver dozens of proteins into plant host cells, we predict that this is a common conduit by which bacteria invade host cells. Once inside a host, conditions are typically much better for bacterial growth, reproduction, and proliferation (Beattie and Lindow 1995, 1999; Lindow and Brandl 2003).

4.2 Fungi

While grass-associated clavicipitaceous fungal endophytes (Class I, see Box 1) typically colonize the entire host plant systemically via vertical transmission (e.g., seed), tree-associated fungi (Classes II and III, see Box 1) typically colonize roots and leaves via horizontal transmission. Fungi can directly enter roots or leaves via plant epidermal cells by extending hyphae on top of, between, or through plant cells (Jones and Dangl 2006; Rodriguez et al. 2009). Like bacteria, openings in leaves (e.g., stomates) or roots (e.g., root hairs) may facilitate fungal invasion (e.g., Arnold and Herre 2003; Agrios 2005). In addition, fungi evade or manipulate plant host chemical pathways to gain entry (Van Bael et al. 2017). Lastly, damage caused by leaf-chewing insects may provide a conduit for fungi to enter leaves. For example, Arnold (2008) demonstrated that foliar damage caused by hesperlid larvae almost doubled endophyte infection among leaves of the tree *Gustavia superba* in a Panamanian forest. Ultimately, once inside the leaf, fungal hyphae typically grow into the intercellular spaces of the mesophyll or the apoplast where they function as mutualists or pathogens (Giraldo and Valent 2013).

5 The Impacts of Microbial Endophytes on Plant Hosts

5.1 Beneficial Endophytes

5.1.1 Plant Growth Promotion

A diverse array of endophytes, typically root-associated bacteria, commonly fix nitrogen and synthesize plant hormones that stimulate plant growth, reproduction, and tissue differentiation (recently reviewed by Denance et al. 2013; Gaiero et al. 2013; Brader et al. 2014; Santoyo et al. 2016). Rhizobia (Alphaproteobacteria) and actinorhizal bacteria (Actinomycetales) occupy root nodules of leguminous trees (Fabaceae), which are relatively abundant in tropical forests, and fix nitrogen for hosts in exchange for carbon (Gentry 1988; Hedin et al. 2009; Vitousek et al. 2013).

Several other bacterial root endophytes—primarily Proteobacteria and Firmicutes—also fix nitrogen, though the degree to which plants tap this source of N is unknown (e.g., Baldani et al. 1997; Reinhold-Hurek and Hurek 1998; Dalla Santa et al. 2004). In recent studies of two temperate conifer species (using high throughput sequencing), Carrell and Frank (2014, 2015) discovered that up to half of conifer needle endophytes were nitrogen-fixing bacteria. In another study, Moyes et al. (2016) detected significant nitrogenase (the enzyme which fixes nitrogen) activity among bacterial endophytes in *Pinus flexilis* needles, and moreover this nitrogen readily diffused into needles. Though foliar endophytes likely fix less nitrogen compared to rhizobial bacteria in root nodules, it may ultimately be more cost-effective for plants to support foliar nitrogen fixers compared to root nodule bacteria which are costly (reviewed by Vitousek et al. 2013). In addition to fixing nitrogen, it is common for plant-associated bacteria and fungi to function as mutualists and produce plant hormones such as gibberellins, cytokinins, and auxins that stimulate root and leaf growth and aid in wound repair (e.g., Lindow et al. 1998; Robinson et al. 1998; Gutierrez-Manero et al. 2001; Maor et al. 2004; Bhore et al. 2010; reviewed by Strack et al. 2003; Spaepen et al. 2007). In fact, over 80% of root bacterial endophytes produce indole-3-acetic acid (IAA), an auxin that stimulates plant tissue differentiation thereby indirectly increasing plant growth (Ramos Solano et al. 2008; Davies 2010). IAA producing-endophytes are phylogenetically widespread among at least 3 phyla of bacteria as well as 3 phyla of fungi, all of which have been isolated from tropical trees (Schmelz et al. 2003; Yang et al. 2006; Spaepen et al. 2007; Bajo et al. 2008; Rodriguez et al. 2009; Davies 2010; Hoffman et al. 2013; Griffin and Carson 2015). Thus, it is likely that tree endophytes in tropical forests commonly fix nitrogen and produce hormones for their plant hosts. Alternatively, however, if these hormones stimulate plant tissue differentiation in times of stress or when resources are low, these hormones may be, to some degree, deleterious.

5.1.2 Pathogen Protection

i. *Bacteria*

Bacterial endophytes protect plant hosts from bacterial and fungal pathogens primarily by competitive exclusion and antimicrobial production. Endophytes typically occupy an ecological niche similar to pathogens, and early studies hypothesized that endophytes decreased pathogen abundance via competitive exclusion (reviewed by Hallmann et al. 1997). In this case, competition may occur simply via priority effects whereby benign or beneficial pathogens arrive at and occupy niche space, making it unavailable for pathogens (e.g., Wilson and Lindow 1994; Ji and Wilson 2002; Innerebner et al. 2011). In addition, more recent studies have demonstrated that endophytes synthesize secondary metabolites such as alkaloids, flavonoids, phenols, terpenoids, and xanthones, which inhibit pathogen growth and persistence (reviewed by Strobel et al. 2004; Brader et al. 2014; Nisa et al. 2015). Actinomycetes, which comprise ~20% of all endophytes identified to date, alone synthesize almost half of the world's known antimicrobial compounds (Berdy 2005; Waksman et al. 2010; Berdy 2012; Hardoim et al. 2015). In a recent study across five species of tropical tree seedlings, Griffin (2016) demonstrated that nearly half of all foliar endophytes were actinomycetes. Though speculative, we suggest that a critical function of endophytic actinomycetes is a key mutualism whereby they provide antimicrobial agents in exchange for shelter, carbon, or other nutrients from their plant hosts. This is functionally analogous to how Myrmecophytic plants provide domatia and extrafloral nectaries for their ant mutualists in exchange for protection from herbivores (Janzen 1966; Gaume et al. 1998; Heil and McKey 2003). We hypothesize that this is common function of Actinomycetes and their host trees for numerous tree species in tropical forests.

ii. *Fungi*

Fungal endophytes also competitively exclude pathogens and produce an array of secondary metabolites and antimicrobial compounds that likely offer some degree of protection from fungal and bacterial pathogens. In greenhouse and field experiments in Panama, *Colletotrichum tropicale* (Sordariomycetes), the dominant foliar endophyte among at least 10 tropical tree species, reduced pathogen damage among *T. cacao* seedlings by 10–80% compared to endophyte-free controls (Arnold et al. 2003; Hyde et al. 2009; Rojas et al. 2010; Cannon et al. 2012; Christian et al. 2017b). The mechanisms by which *C. tropicale* decreased pathogen damage were not evaluated. In another study, Mejia et al. (2008) demonstrated that 48% of culturable endophytes isolated from *T. cacao* leaves competitively excluded at least one of three dominant fungal pathogens in vitro. In addition to competitive exclusion, fungal endophytes decrease pathogen damage by producing antimicrobial compounds. Schulz et al. (2002) demonstrated that ~80% of 6,500 fungal endophytes from temperate and tropical herbaceous plants and trees synthesized antimicrobial or antifungal compounds in vitro. In all, nearly 5,000 secondary metabolites have been isolated from fungal endophytes, half of which are polyketides, but also include terpenoids, steroids, and phenols (reviewed by Gunatilaka 2006; Berdy 2012; Ludwig-Muller 2015; Nisa et al. 2015). Polyketides, in particular, include antimicrobial compounds and mycotoxins that higher plants produce to defend themselves against pathogens (Dixon 2001; Flores-Sanchez and Verpoorte 2009). Though it is clear that fungal endophytes commonly produce antimicrobial compounds, empirical studies demonstrating that these compounds are induced via endophyte-pathogen interactions are lacking. One study however used metabolomic approaches to demonstrate that a temperate pine tree endophyte, *Paraconiothyrium variabile* (Coelomycetes), produced metabolites to inhibit *Fusarium oxysporum* (Sordariomycetes) growth only *after* exposure to the pathogen (Combes et al. 2012).

iii. *Endophytes induce host resistance to pathogens*

There is increasing evidence that both bacterial and fungal endophytes can trigger an immune response in host plants (induced systemic resistance) to increase host tolerance to pathogens (Bargabus et al. 2002; Bargabus et al. 2004; Tran et al. 2007; Verhagen et al. 2010; Brotman et al. 2012; Desoignies et al. 2013; Mejia et al. 2014). Endophytes may ramp up host resistance to combat future pathogen or insect attack (reviewed by Pineda et al. 2010; Zamioudis and Pieterse 2012; Bakker et al. 2013; Pieterse et al. 2014). This mutualism is particularly common among bacteria in the genera *Pseudomonas* (Gammaproteobacteria) and *Bacillus* (Bacilli), which are some of most common taxa isolated from tropical tree species (Lambais et al. 2006, 2014, 2017; Kembel et al. 2014). For example, Van Peer et al. (1991) were the first to demonstrate that root colonization by the bacterium *Pseudomonas fluorescens* enhanced carnation (*Dianthus caryophyllus* L.) resistance to the fungal pathogen *F. oxysporum*. Since then, over 100 studies have been published that have demonstrated the ability of bacterial strains to systemically induce host resistance to pathogens in other portions of the plant (reviewed by Pieterse et al. 2014; Griffin and Carson 2015). Though not many cases of systemically induced host resistance exist for fungi, Mejia et al. (2014) recently demonstrated that colonization of the fungal endophyte *Colletotrichum tropicale* inside *T. cacao* leaves caused the up-regulation of pathogen-resistance genes. Because *Colletotrichum* is a dominant fungal endophyte, this phenomenon may be more common among fungal endophytes than previously thought.

5.1.3 Herbivore Protection

Endophytes commonly reduce herbivore damage by activating plant defense pathways or by altering enemy behavior. For example, tomato root inoculations with the bacterium *Bacillus subtilis* reduced egg masses of a root-knot nematode. These nematodes damage tomato roots and exacerbate *Fusarium* pathogen infection by 40–62% (Adam et al. 2014). For fungi, vertically transmitted grass endophytes decrease host susceptibility to insects and even mammalian herbivores by as much as 55% (Clay and Schardl 2002; Schardl et al. 2004; Saikkonen et al. 2010; Tanaka et al. 2012; Faeth and Saari 2012). In a meta-analysis of 99 papers, Saikkonen et al. (2010) concluded that grass endophytes typically function to deter herbivores; however, there was no overall relationship between tree endophytes and herbivore damage. More recent studies, however, have revealed that fungal endophytes can either directly decrease herbivore survival rates or indirectly decrease their fecundity, alter foraging behaviors or the gut microbiome, or even increase their susceptibility to predation (Marcelino et al. 2008; Van Bael et al. 2009; Jaber and Vidal 2010; Bittleston et al. 2011; Estrada et al. 2013; Hammer and Van Bael 2015). For example, studies of leaf-cutter ants (*Atta* and *Acromyrmex)* demonstrated that fungal endophytes alter leaf selection and ant behavior (Van Bael et al. 2012; Coblentz and Van Bael 2013; Estrada et al. 2013; Estrada et al. 2015). In a Panamanian forest, Van Bael et al. (2012) demonstrated that ants took 30–40% longer to cut, carry, and clean leaves with higher fungal endophyte abundance and diversity compared to leaves with lower abundance and diversity. Moreover, at the same site, ants selected leaves that on average hosted 20–33% fewer fungal endophytes compared to surrounding leaves (Coblentz and Van Bael 2013). These findings are important because leaf-cutter ants defoliate leaves of ~60% of woody species in Neotropical forests and cut 12–17% of the total leaf area produced by trees (Cherrett 1968; Rockwood 1976; Blanton and Ewel 1985; Holldobler and Wilson 2010). Overall, these results suggest that fungal endophytes likely regulate herbivore foraging and damage.

5.2 Pathogens

Plant pathogens gain access to host cells using highly evolved mechanisms, where they then proliferate and cause disease. Like mutualists, pathogenic bacteria can enter plant tissue through openings (e.g., stomates, trichome bases, wounds) and proliferate in intercellular spaces (reviewed by Griffin and Carson 2015). Fungal pathogens and the fungal-like protist oomycetes can enter directly via epidermal cells or through feeding structures called haustoria, which function to invaginate plant cell membranes (reviewed by Jones and Dangl 2006; Dean et al. 2012; Jiang and Tyler 2012; Pawlowski et al. 2012; Thines 2014). Both bacteria and fungi use highly adapted secretion systems to deliver effector proteins into plant cells to break down host cell walls, facilitate dispersal of microbes on and inside plant tissues, and bypass plant immune responses (Jones and Dangl 2006; Ellis et al. 2009; Stergiopoulos and de Wit 2009; Wooldridge 2009). Fungi and oomycetes can do this either in the extracellular matrix formed along epidermal cells or once inside host cells, whereas bacteria must deliver effectors inside cells (Jones and Dangl 2006). Once effectors are delivered, pathogens can feed on dead host cells (necrotrophs) or invade quickly and extract nutrients from hosts without killing them (biotrophs), however many of the most prolific pathogens can display both lifestyles (Glazebrook 2005; Jackson 2009; Dean et al. 2012; Mansfield et al. 2012). Successful pathogens are able to either suppress or evade detection and cause damage to plant tissue.

5.2.1 Bacterial Pathogens

Though the impacts of bacterial pathogens in tropical forests are not well documented, evidence from agricultural systems suggests that these organisms likely cause severe damage even in more diverse systems. Some of the most potent bacterial pathogens in the world occur in the tropics and diminish agricultural yields. For example, *P. syringae* has commonly been isolated from plants in Fabaceae, one of the most commonly represented families in tropical forests (Horst 1990; Sarkar and Guttman 2004; Silby et al. 2011; Morris et al. 2013; reviewed by Griffin and Carson 2015). Moreover, *Xanthomonas* (Gammaproteobacteria) is a largely pathogenic bacterial genus whose members reduce tropical crop yields, including banana, citrus, rice, and sugarcane, by over 50% (Biruma et al. 2007;

Tripathi et al. 2009; Ryan et al. 2011). Three *Xanthomonas* species (*X. axonopodis*, *X. campestris, X. oryzae*) are among the top ten most "scientifically and economically important" plant pathogenic bacteria in the world. Four of the other ten, two *Dickeya* (Gammaproteobacteria) spp. and two *Pectobacterium* (Gammaproteobacteria) spp., together cause disease in half of all angiosperm plant orders (Ma et al. 2007). If endophytes are primarily pathogenic and tree host species are differentially vulnerable, then endophytes may be major agents of forest turnover particularly in small size classes and in areas around parent trees (see "The impacts of endophytes on tropical tree communities" section below).

5.2.2 Fungal Pathogens

Fungal pathogens typically lie within the phyla Ascomycota and Basidiomycota and cause more damage to hosts in tropical than in temperate systems. For example, seven of the top ten most "scientifically and economically important" fungal pathogens lie within Ascomycota, while the remaining three lie within Basidiomycota (Dean et al. 2012). The most destructive agricultural plant pathogen globally is the rice blast caused by *Magnaporthe oryzae* (Sordariomycetes), which destroys enough rice to feed more than 60 million people annually (Scardaci et al. 1997). Though particular species actually function as mutualists (see above), many *Colletotrichum* spp. (Sordariomycetes) are particularly damaging to tropical crop species, where they can cause up to 100% mortality among banana, cassava, sorghum, and rubber trees (Prusky 1996; Cao et al. 2017). In general, pathogens in tropical systems decrease crop yields 50–100% more than temperate pathogens, and moreover outnumber temperate pathogens 10:1 (Wellman 1968; Wellman 1972; Hill and Waller 1982; Shivas and Hyde 1997; Thurston 1998; Gilbert 2005). In the first studies on plant-pathogen interactions in tropical forests, Augspurger and colleagues found that damping-off disease caused by *Pythium* (Oomycetes) spp. was the leading cause of seedling mortality for six of nine tree species in Panama (Augspurger 1983; Augspurger and Kelly 1984; Augspurger 1984; Kitajima and Augspurger 1989). In Neotropical forests, foliar fungal pathogens cause damage to over three-fourths of shrub and tree species, and the degree of damage ranges from 1–34% of entire leaf area (N = 78 species; Gilbert 1995; Barone 1998; Benitez-Malvido et al. 1999; Garcia-Guzman and Dirzo 2001). Indeed, even small levels of damage to tropical seedlings are not trivial, because as little as 8% of leaf damage can cause up to 100% seedling mortality (Clark and Clark 1985; reviewed by Coley and Barone 1996). Thus, fungal pathogens in tropical systems cause significant damage to plant hosts and have broad implications for plant communities at larger scales.

5.3 Endohyphal Bacteria—Good or Bad for Plant Hosts?

Recent studies have demonstrated that fungal endophytes can harbor bacteria within their hyphae, which together can increase or decrease host plant performance (Partida-Martinez and Hertweck 2005; Partida-Martinez et al. 2007a; Salvioli et al. 2010, 2016; Hoffman et al. 2013; reviewed by Bonfante and Anca 2009). Fungi that host endobacteria are phylogenetically diverse, including members of Mucoromycotina, Mortierellomycotina, Glomeromycota, Basidiomycota, and Ascomycota. Surprisingly, to date, however, endohyphal bacteria are exclusively found in Proteobacteria (Barbieri et al. 2000; Bianciotto et al. 2003; Bertaux et al. 2005; Partida-Martinez et al. 2007b; Sharma et al. 2008; Sato et al. 2010; Desiro et al. 2015). For example, the plant mutualist mycorrhiza *Gigaspora margarita* (Glomeromycota) harbors the bacterium *Candidatus Glomeribacter gigasporarum* (Betaproteobacteria) in densities of 250,000 cells per fungal spore, and when this bacterium is present it enhances fungal establishment and growth (Bianciotto et al. 1996, 2003, 2004). Conversely, the fungal root endophyte *Rhizopus microsporus* (Mucorales) harbors the bacterium *Burkholderia rhizoxinica* (Betaproteobacteria), which causes rice blast disease only when both the bacterium and fungus are present (Partida-Martinez and Hertweck 2005; Partida-Martinez et al. 2007b). In another study, Hoffman et al. (2013) demonstrated that the foliar fungal endophyte *Pestalotiopsis aff. neglecta* (Sordariomycetes) isolated from a temperate coniferous tree (*Platycladus orientalis*) produced ∼ 5 times more plant hormones when its endohyphal bacterium *Luteubacter* (Gammaproteobacteria) spp. was also present. Moreover, *P. orientalis* shoot and root length increased by ∼30–33% when the bacterium was present inside the fungal endophyte. Though studies have been limited in scope, multi-trophic interactions among fungi, bacteria, and plant hosts are likely common among higher plants. For example, Shaffer et al. (2016) recently found that 75% of seed and foliar fungal endophytes hosted at least one endohyphal bacterium among 26 tropical angiosperm species. Clearly, more studies are needed to understand the breadth and implications of these very complex microbe-microbe-plant interactions. Specifically, we propose that future studies address the prevalence and impacts of predatory bacteria (those that kill and digest other bacteria) and bacteriophages (viruses that infect bacteria) among tree-associated endophyte communities (Box 2).

Box 2. Predatory bacteria and bacteriophages: 2 new areas on the horizon

Predatory bacteria and bacteriophages are abundant organisms that occur in nature and may be critical components of plant ecology. It has been known for decades that "predatory" bacteria (e.g., *Bdellovirbio*, *Micavibrio*, *Myxobacteria*) kill and digest other gram-negative bacteria (reviewed by Negus et al. 2017). Specifically, *Bdellovibrio* (Deltaproteobacteria) bacteria colonize the space between the cytoplasmic membrane and outer membrane (periplasm), where they feed on the host cell's proteins and nucleic acids and ultimately kill host cells from the inside out (Sockett 2009). *Micavibrio* (Alphaproteobacteria) bacteria attach to the exterior of a prey bacterium and remain attached as they divide, eventually draining their host to death (a.k.a. the "vampire" bacteria). *Myxobacteria* (Deltaproteobacteria) hunt other bacteria as social swarms, releasing enzymes into the environment to digest their prey (Velicer and Vos 2009). Though these predator-prey interactions have almost exclusively been demonstrated in water and in soil, scientists have recently suggested that predatory bacteria may be common inside mammalian hosts (Dashiff et al. 2011; Negus et al. 2017). We hypothesize that this may also commonly occur among plant hosts in tropical forests because water and soil are both major sources of plant endophytes (see "What structures endophyte communities?" above). Moreover, Alphaproteobacteria and Deltaproteobacteria are two of the most common classes on and inside leaves of tree species in Panama (Kembel et al. 2014; Griffin 2016). Perhaps even more ecologically important than predatory bacteria, bacteriophages (Greek for "eaters of bacteria"), or viruses that infect bacteria, are the most abundant organisms on Earth and are estimated to infect up to 70% of bacterial cells globally (Tortora et al. 2016; Willey et al. 2016). Though bacteriophages are of particular interest in agriculture where they can be genetically engineered to control plant bacterial pathogens (Frampton et al. 2012; Pires et al. 2016), their prevalence in more natural systems and their basic ecology remain underexplored. Knowing that the plant microbiome is a cryptic driver of plant community dynamics at large scales (see "The impacts of endophytes on tropical tree communities" section), microbe-microbe interactions (e.g., endohyphal bacteria, predator-prey bacteria, bacteriophage-bacteria) may prove to be the true drivers of plant community structure and function.

6 The Impacts of Endophytes on Tropical Tree Communities

6.1 Negative Density Dependence of Pathogens Maintains Tree Community Diversity

Specialist pathogens may act as a stabilizing force to promote and maintain plant diversity by reducing host fitness in areas close to reproductive adults or when host density is high (Gillett 1962; Janzen 1970; Connell 1971). Simply put, pathogens that are host-specific can cause a reduction in the competitive abilities of particular plant species and allow other plant species to co-occur (Janzen 1970; Connell 1971; reviewed by Carson et al. 2008). Studies demonstrating host-specificity of pathogens and frequency-dependent tree mortality have been observed numerous times in the tropics, primarily for insect pests and fungal pathogens (e.g., Mangan et al. 2010; Bagchi et al. 2014; reviewed Carson et al. 2008; Mordecai 2011; Comita et al. 2014; Sarmiento et al. 2017). Augspurger and colleagues conducted the first empirical tests of the Janzen-Connell hypothesis for pathogens and demonstrated that oomycete pathogens were host-specific and their impacts were greater in areas of higher seedling density closer to parent trees (Augspurger 1983, 1984; Kitajima and Augspurger 1989). Since these studies, numerous others have shown similar patterns among oomycetes and fungal pathogens in tropical forests (Gilbert et al. 1994; Gilbert and De Steven 1996; Gilbert et al. 2001; Gilbert and Webb 2007; Comita et al. 2010; Mangan et al. 2010; Bagchi et al. 2014). La Manna et al. (2017) recently demonstrated that negative density dependence is stronger for rare tree species in tropical forests compared to rare temperate species, which may function to maintain hyper-diversity of tropical tree communities. Not a single study, however, has determined whether this pattern exists for pathogenic bacteria. In the first study of its kind, Griffin et al. (2016) found that seedlings of three of five tree species grew up to 49% more after experimentally reducing their foliar bacteria in situ for three years in a tropical forest in Panama. These results demonstrate that the net effect of these bacteria were pathogenic (though bacterial reductions increased growth for one species). If this is true, the implications for the maintenance of species diversity in tropical forests are clear: enemies may build up around conspecifics of particular species and reduce their performance and dominance.

6.2 *Endophytes Can Partition the Plant Fundamental Niche to Enhance Tree Diversity*

Microbial endophytes below- and above-ground may provide an important yet cryptic dimension of niche differentiation for plant communities at large scales. Though soil resource and light gradients have been associated with species-specific trade-offs required for niche partitioning (Clark et al. 1998; Condit et al. 2000; Harms et al. 2001; reviewed by Wright 2002; Kitajima and Poorter 2008), it remains unclear how these abiotic factors facilitate the coexistence of hundreds of tree species in tropical forests (e.g., Hubbell et al. 1999; Hubbell 2001; Chave 2004; Silvertown 2004). Plant-associated microbes, however, may function as a stabilizing force to increase differences in species' performance outcomes (i.e., niches) along gradients or among interactions with other trophic levels (e.g., Chesson 2000; Bever et al. 2010; Mordecai 2011). In this framework, such stabilizing processes cause intraspecific effects to be more negative than interspecific differences (Chesson 2000). Thus, when any single species increases in abundance, its per capita growth rate slows relative to other species, which aids in species coexistence (Chesson 2000). Recently, Griffin et al. (2016, 2017) found that foliar bacteria caused co-occurring plant species to perform quite differently within contrasting soil nutrient resource levels suggesting that the interplay between plant microbes and soil fertility can create a cryptic and fairly narrow niche early in ontogeny. Ultimately, plant-microbe interactions may more finely partition niche space among coexisting plant species and thus function to maintain plant diversity.

7 Conclusions and Future Directions

Bacterial and fungal endophytes are diverse and important drivers of plant performance and may be critical components of tropical tree community composition and structure. On one hand, endophytes may directly increase host performance by producing plant hormones or confer protection to hosts from pathogens and other enemies via competitive exclusion, metabolite production, or by inducing plant systemic resistance to enemies. On the other hand, endophytes may function as pathogens and decrease plant host performance, which may have important implications for plant communities. Recent studies have demonstrated that bacterial-fungal interactions, notably interactions between fungal endophytes and their endohyphal bacteria, can either strengthen mutualist interactions between plants and microbes or together cause disease. Thus, endophytes comprise a cryptic and complex dimension of trophic interactions within plant communities and empirical studies are needed to unravel this complexity.

Tropical endophytes should be a major research focus moving forward. Indeed, recent developments in high-throughput sequencing technologies, specifically next-generation sequencing and "-omics" approaches, have allowed us to address more questions about the complex interactions between endophytes and plant hosts. Thus, it is clear that our understanding of endophyte-host interactions, particularly among tropical trees, is still in its infancy. Moreover, recent studies have demonstrated that microbe-microbe interactions such as mycorrhizal fungi-endohyphal bacteria, predator-prey dynamics among bacteria, and bacteriophage-bacteria interactions are common and may ultimately be critical for endophyte community structure and function. In particular, we propose two interesting and novel areas moving forward: 1. Testing the prevalence and impacts of 1. Bacteriophages that protect plant hosts via antibiotics; and 2. Predatory bacteria that colonize plants or possibly even plant-associated bacteriophages that consume bacteria (Box 2). If these interactions are common and widespread, the interactions that occur among microbes may be key to understanding ecological processes and plant community dynamics. Recent reviews have posited that plant-associated microbes should be model systems to test important community-level ecological theories such as succession, competition, and community assembly (Meyer and Leveau 2012; Christian et al. 2015; Griffin and Carson 2015). Notable goals of future research include 1. Quantify the costs and trade-offs associated with trees hosting "beneficial" endophytes among tropical trees; 2. Evaluate the degree to which endophytes produce antimicrobial compounds and empirically determining the degree to which fungal endophytes protect tropical tree hosts via systemic induced resistance in situ; 3.

Begin to empirically evaluate the ecological impacts of microbe-microbe interactions on plant host performance and ultimately plant community dynamics. Ultimately, we are just beginning to scratch the surface of our understanding of the plant microbiome, and scientists should be excited to disentangle the complexities of one of the last frontiers of biodiversity.

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