Bot. Rev. (2015) 81:105–149
DOI 10.1007/s12229-015-9151-9

The Ecology and Natural History of Foliar Bacteria with a Focus on Tropical Forests and Agroecosystems

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Abstract Leaves of higher plants comprise perhaps the largest bacterial substrate on earth, yet we know very little about the bacteria that occupy these spaces. In this review, we first examine the ecology and behavior of bacteria that reside on leaf surfaces. Next, we discuss the ecological implications of foliar bacteria that reside in interior portions of leaf tissues. Later, we consider the studies on foliar bacteria in tropical habitats to date. Finally, we examine evidence regarding the potential roles of foliar bacteria in structuring tropical plant communities. Bacteria colonize the phyllosphere via animal vectors or passively from soil, wind, or rain, though there are too few data to determine the relative contributions of these sources to the phyllosphere. Additionally, the degree to which parent plants transmit bacteria to offspring via seed remains unknown. We predict that high temperature, high humidity, low UV radiation, and leaf architecture in the tropical understory enable tropical leaves to support more abundant and diverse bacterial communities compared to temperate leaves. While the extent of competitive interactions among bacteria remains poorly resolved, evidence from agricultural crop species and *Arabidopsis thaliana* suggests that these interactions cause niche partitioning based on carbon use. The degree to which phyllobacteria and endophytes of tropical plants are pathogenic versus mutualistic or neutral remains unexplored. We hypothesize, however, that the detrimental impact of bacterial pathogens ultimately increases as the abundance of single host tree species increases, which can promote and maintain plant diversity in tropical forests.

Resumen Las hojas de las plantas superiores constituyen posiblemente el sustrato bacteriológico más extenso en el planeta, sin embargo sabemos muy poco sobre las bacterias que ocupan estos espacios. En este artículo examinamos, en primer lugar, la ecología y el comportamiento de las bacterias que residen en las superficies de las hojas. Luego, discutimos las implicaciones ecológicas de las bacterias foliares que residen en el interior de los tejidos de las hojas. Además, consideramos los estudios sobre bacterias foliares en hábitats tropicales a la fecha. Finalmente examinamos la evidencia que existe sobre el potencial impacto de las bacterias foliares en la estructura de comunidades de plantas tropicales. Las bacterias generalmente colonizan la filosfera a través de vectores animales o pasivamente a través del suelo, el viento o la lluvia, aunque hay poca información para determinar la contribución relativa de estas fuentes a la filosfera. Adicionalmente, no se sabe hasta qué punto ocurre una transmisión bacteriana de progenitor a progenie a través de semillas. Predecimos que las altas temperaturas, la elevada humedad, la baja radiación ultravioleta, y la arquitectura de las hojas en el sotobosque permiten que las hojas tropicales contengan comunidades bacteriológicas más abundantes y diversas en comparación con hojas de clima templado. Aunque el grado de interacciones competitivas entre bacterias aún no ha sido bien entendido, evidencia de especies de interés agronómico y *Arabidopsis thaliana* sugiere que estas interacciones causan particiones de nicho basadas en el uso de carbono. La naturaleza patógena, mutualista o neutra de las filobacterias y bacterias endófitas de plantas tropicales no se ha explorado hasta el momento. Nuestra hipótesis es, sin embargo, que el impacto negativo de patógenos bacterianos es mayor con el incremento en la abundancia de huéspedes específicos, lo que puede promover y mantener la diversidad de plantas en los bosques tropicales.

Keywords Foliar bacteria · Tropical forests · Agroecosystems · Plant diversity · Microbial ecology · Plant coexistence · Endophytes · Pathogens

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Introduction

Sometimes referred to as the “great unseen,” bacteria are by far the most abundant organisms on Earth (4–6*10^30 individuals) and represent the largest organic pool of nitrogen and phosphorus (Whitman et al., 1998). Comprising a global biomass of 350,000–550,000 million tonnes (Whitman et al., 1998), bacteria outweigh invertebrates by orders of magnitude and exceed the biomass of all plants and animals on Earth (Groombridge & Jenkins, 2002; Hogan, 2010). If, as Wilson (1987) argued, invertebrates are the “little things that run the world,” we argue that by their sheer abundance and biomass alone, bacteria have as much, if not more, of a function in worldwide ecology.

Whereas soil microbial communities and their effects on plants have received extensive attention, (Mills & Bever, 1998; Packer & Clay, 2000; Reynolds et al., 2003; Bever, 2003; Falkowski et al., 2008; van der Heijden et al., 2008; Mangan et al., 2010; Maron et al., 2011; Schnitzer et al., 2011; van der Putten et al., 2013), relatively little is known about foliar bacteria and their interactions with plants in nature. Yet bacteria are by far the most abundant colonizers of the leaf surface, occurring at densities of up to 10^7 cells/cm^2 on leaves (Lindow & Brandl, 2003; Delmotte et al., 2009). Moreover, the global leaf surface area (upper and lower leaf surface) may be one of the largest microbial habitats at over 1 billion km^2 (Morris & Kinkel, 2002; Vorholt, 2012), which is two times larger than the earth’s surface area (510 million km^2: CIA, 2010).

Though studies from agricultural systems and plantations are more common, the degree to which foliar bacteria benefit or are detrimental to wild plants remains little studied, particularly in the tropics (see Gilbert, 2002; Ghazoul & Sheil, 2010). The degree to which bacteria-plant interactions are comparable between non-wild and wild systems remains unclear. For example, major differences in the phylogenetic diversity and species composition of plant hosts likely occur among temperate agroecosystems, tropical agroecosystems, and tropical forests. In addition, major differences almost certainly exist among these systems, particularly in terms of their microbial communities, canopy structure, and disturbance regimes.

Nevertheless, we use findings from agricultural systems as a means to guide our hypotheses and predictions and to inform us about the diversity, abundance, and potential impact of foliar bacteria in tropical forests. That being said, only a handful of studies have examined tropical foliar bacteria in the wild (see Lambais et al., 2006; Fürnkranz et al., 2008; Li et al., 2008; Qin et al., 2012; Kembel et al., 2014), and even the basic ecology of these organisms remains fertile ground for research. Here, we first examine the ecology and behavior of bacteria that reside on the leaf surface. Next, we discuss the ecological implications of foliar bacteria that reside in interior portions of leaf tissues. Later, we consider studies on foliar bacteria in tropical habitats to date. Finally, we examine evidence regarding the potential roles of foliar bacteria in structuring tropical plant communities.

Definitions

We modify Beattie and Lindow's (1999) definition of "phyllobacteria" and restrict it to those bacteria that live and persist on the leaf surface without being harmful or parasitic. This includes mutualistic and commensal taxa. They are true epiphytes (Kricher, 2011), functionally defined in part by not colonizing the interior of leaf tissues (though the proportion that remain solely on the leaf surface and never colonize the leaf interior is unknown). Thus we distinguish epiphytic phyllobacteria from bacterial endophytes and pathogens. Though we acknowledge that many microbiologists define endophytes as only those found inside plant tissues and function as mutualists (and typically not pathogens) to their plant hosts (reviewed by Wilson, 1995; Stone et al., 2000; Schulz & Boyle, 2006), we define bacterial endophytes as bacteria that reside inside leaves and are commensal, mutualistic, or pathogenic (Box 1). Pathogens and endophytes may colonize the leaf surface via horizontal transmission (e.g., passively, by factors such as wind or rain, or via animal vectors), or via vertical transmission (from a parental plant to offspring via seed or by raining down from a mother plant to offspring: Ewald, 1987), but they must reach the leaf's interior before they can cause disease or function as mutualists (Beattie & Lindow, 1995; Gnanamanickam, 2006). Last, we define "core microbiome" as a subset of ecologically important microbial taxa commonly shared among individuals of a single plant species or shared among multiple plant species living in the same habitat, community, or region (Shade & Handelsman, 2012).

Box 1 What is an endophyte?

The term "endophyte" has been extant in the literature for almost 140 years. De Bary (1866) was the first to define "endophyte" as "any organisms occurring within plant tissues." Over time, however, many definitions for endophyte have been used (see review by Hyde & Soytong, 2008), though the most commonly used is Petrini's definition (1991). Petrini (1991) 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." Bacteria (as well as fungi), though, may have dormant or latent phases inside leaf tissue before causing disease to plant hosts, which Wilson (1995) characterized as the "continuum of infection patterns." Thus, under this definition bacteria that are clearly pathogens may be considered mutualistic endophytes (Schulz & Boyle, 2006). For example, Bashan and Okon (1981) demonstrated that tomato plants grown in *P. syringae* infested soil were symptomless but produced up to 30 % less foliage than plants in sterile soil! We therefore side with De Bary (1866) and more recently Henis and Bashan (1986) and define foliar bacterial endophytes in this review as bacteria that have colonized the interior portions of leaf tissue.

Bacterial Colonization and Recruitment to the Phyllosphere

From Soil to Seed to Seedling

The origin of the bacteria that colonize the phyllosphere remains unclear (Bulgarelli et al., 2013), but some may originate from the surface of the seed. The seed surface harbors bacteria, which are transmitted to the emerging cotyledon during germination (Maude, 1996; Nelson, 2004; Gitaitis & Walcott, 2007). Seeds reside in soil, which is a rich habitat for bacteria. For example, Horner-Divine et al. (2003) estimated the abundance of bacteria to be 10^8 in a single gram of soil. In another study, 10 g of soil hosted $8.3 * 10^6$ bacterial species (Gans et al., 2005). Indeed, evidence suggests that seeds “recruit” bacterial populations via seed exudates, some of which may make up the core microbiome that reach the phyllosphere upon germination (Vorholt, 2012). For instance, seeds release a variety of exudates, many of which can either inhibit bacterial pathogens or attract beneficial bacteria to ward off pathogens (reviewed by Nelson, 2004; for seed endophytes that colonize the rhizosphere see Johnston-Monje & Raizada, 2011; Links et al., 2014). Furthermore, naturally-occurring seed endophytes have been isolated from coffee (Vega et al., 2005), Norway spruce (Cankar et al., 2005), rice (Tripathi et al., 2006), and rapeseed (Granér et al., 2003), though little is known about their ecology (but cf Mastretta et al., 2009). Additionally, bacterial pathogens are known to be seedborne (Maude, 1996; Gitaitis & Walcott, 2007). For example, over 60 species of pathogenic bacteria, representing 5 genera, transmit from seed to seedling in the 100 host crop species studied to date; however, these studies have been largely concentrated in temperate regions (Neergaard, 1977; Phatak, 1980). Because tropical soils are often acidic they may harbor less abundant and diverse bacterial communities compared to temperate soils (Baath & Anderson, 2003; Fierer & Jackson, 2006; Lauber et al., 2009; Rousk et al., 2010). Nonetheless, tropical seeds are still exposed to an enormous abundance of soil bacteria. The few studies characterizing tropical seed microbiomes focus exclusively on fungal communities and all but ignore bacterial communities (reviewed by Gilbert, 2002; Dalling et al., 2011; but cf Gallery et al., 2010; Garcia et al., 2013; Zalamea et al., 2015). Empirical studies are needed to determine the degree to which soil bacteria infect seeds and go on to colonize the phyllosphere after germination.

Mechanical Chauffeuring

When a young developing shoot emerges from the soil it may contact bacteria on the surface of the seed or in the soil and thereby mechanically transport bacteria onto the phyllosphere. We term this *mechanical chauffeuring*. Free-living bacterial pathogens in temperate soils in agroecosystems may fail to survive for more than a few days (Schaad & White, 1974; Schuster & Coyne, 1974; McCarter et al., 1983; Goodnow et al., 1990; Kocks et al., 1998). Still, Bacterial survival may be longer in tropical soils, which remain moist and warm throughout much of the year. Indeed, bacterial pathogens of plants can survive on crop residues (e.g., litter, leaf stems) on the ground for up to 8 months and can even overwinter (Ark, 1958; Jones et al., 1986; Legard & Hunter, 1990; Maude, 1996; Zhao et al., 2002). For example, Ark (1958) showed that the gram-negative pathogen *Xanthomonas campestris* overwintered in Oklahoma on cotton debris on the soil surface and infected newly emerging plants the following year. Overall, we suggest that mechanical chauffeuring may be a common avenue by which bacteria colonize plant species in the emerging seedling stage when these plants may be particularly vulnerable to pathogens or when they need their bacterial mutualists early in development.

Wind and Rain

Wind, rain, and overland flow passively carry bacteria, particularly pathogenic ones, to new plant hosts on both small and large scales. Faulwetter (1917) was the first to propose that wind-blown rain was the primary dispersal agent of angular leaf spot (caused by *X. campestris*) among cotton plants in the southern United States. This has since been confirmed for *X. campestris*, as well as *X. citri and X. axonopodis* in citrus and gram-negative *Erwinia carotova* in potato (reviewed by Fitt et al., 1989; Bock et al., 2005; Bock & Graham, 2010). Stall et al. (1980) showed that wind and rain dispersed the pathogen *X. axonopodis* (causal agent of citrus canker) up to 32 m from infected grapefruit trees. In fact, wind and rain caused by hurricanes are thought to be the primary causes of the most recent outbreak of *X. axonopodis* in citrus orchards in Florida (Gottwald et al., 2002; Graham et al., 2004; Irey et al., 2006).

Foliar bacteria may also be dispersed via the water cycle at regional and continental scales. The prominent gram-negative plant pathogen *Pseudomonas syringae* has been found in rain, snow, streams, lakes, and clouds in remote regions throughout Europe, the United States, and New Zealand (Amato et al., 2007; Christner et al., 2008; Morris et al., 2008; 2010). Morris et al. (2008) hypothesized that water runoff regionally disseminates *P. syringae* in both agricultural and natural systems and it can be taken up by aerosols that later precipitate bacteria into other non-adjacent ecosystems. Additionally, Williams (2013) proposed that bacteria in tree pollen can be dispersed via the water cycle. If this is true, it’s possible that many plant-associated bacteria may disseminate via the global water cycle at scales much greater than for the vast majority of larger biota. This strongly suggests that particular plant-associated bacteria will have nearly worldwide distributions, which could lead to much broader host ranges than for taxa with more limited dispersal.

Animal Vectors

Animals, particularly insects, may passively spread bacteria using a variety of mechanisms. Herbivores and other animals (e.g., birds and reptiles) likely vector bacteria via defecation, however to our knowledge there have been no studies for larger animal species. Spreading bacteria via defecation may be particularly prominent in the tropics, where long-distance seed dispersal via defecation is common functions to promote tropical woody species diversity (Howe & Smallwood, 1982; Nathan & Muller-Landau, 2000; Muller-Landau & Hardesty, 2005; Kurten & Carson, 2015). Further, long-range migrating insects traveling to and from tropical regions may facilitate long-distance dispersal of bacteria among host plants across vast regions and among different biomes (reviewed by Chapman et al., 2015). Here, we focus on how insects vector bacteria because this has been the focus of much research. Hemipterans (particularly xylem and phloem tappers) account for more than two thirds of the examples of insect vectoring bacterial pathogens (Nadarasah & Stavrinides, 2011). Their specialized piercing mouthparts often insert bacteria directly into the plant, allowing them to circumvent defenses or the inhospitable environment on the phyllosphere (e.g., Bruton et al., 2003). Chrysomelid beetles also can directly deposit pathogenic bacteria inside leaves but in some cases the bacteria migrate from frass deposited on the leaf and pass through wounds caused by the herbivores (Yao et al., 1996). In other cases, bacteria may be ingested by their insect vector and later spread via saliva (Stavrinides et al., 2009). Finally, bacteria can be transferred on the surface of insects (e.g., antennae and legs) and later deposited mechanically as a byproduct of feeding or pollination (Yao et al., 1996; Hildebrand et al., 2000).

Insects vector bacteria that commonly occur on the phyllosphere of tropical plants, hence insects may commonly mediate phyllosphere community composition. For example, leaf-cutting ants (*Acromyrmex* and *Atta* spp.) in the Neotropics culture and harbor gram-positive *Streptomyces* bacteria; these bacteria function to protect their fungal gardens from pathogenic fungi (Currie et al., 1999; Haeder et al., 2009; Schoenian et al., 2011). Furthermore, individuals from the genus *Streptomyces* frequently produce secondary metabolites, including antibiotics that are widely used in agriculture to primarily kill pathogenic bacteria (Schrey & Tarkka, 2008 for roots; Lauber et al., 2009). *Streptomyces* is the predominant genus in the class Actinobacteria, which is the fifth most common class of bacteria on the phyllosphere among 57 tropical tree species in Panama (Kembel et al., 2014). We hypothesize that during foraging these leaf cutter ants may disperse *Streptomyces* to the plant surface and even high into the canopy where these bacteria may function to ward off pathogens. This idea is intriguing and should be evaluated empirically. In all, we hypothesize that insect vectors shape foliar bacterial communities on the tropical phyllosphere. Testing this hypothesis would require fairly simple experiments where insects are excluded from plants (e.g., via netting) over relevant time frames and the resulting bacterial communities compared to control plants where insects are present.

Vertical Transmission

Phyllosphere bacteria may colonize leaves via vertical transmission, a process by which bacteria are passed from one generation to the next via seed. Bacteria can be transmitted in this manner in three ways: 1. Seeds may be systemically infected via the maternal vascular system 2. Seeds can be indirectly infected from the maternal stigma, where bacteria move through stylar tissues to the embryo. 3. An external infection of maternal flowers or fruits can indirectly infect seeds (Maude, 1996). We also propose that pollen can transmit bacterial pathogens, because pollen is known to contain a variety of antibacterial chemicals that inhibit pathogens in vitro (Basim et al., 2006; Carpes et al., 2007; Morais et al., 2011). The extent to which pathogens as well as mutualists are vertically transmitted and ultimately colonize the seedling phyllosphere is not well understood. Recent studies on grasses and forbes suggest that vertical transmission of fungal mutualists may be common (Cook et al., 2013; Hodgson et al., 2014), though this area remains contentious and research on woody species is lacking (Rodriguez et al., 2009; Sanchez-Marquez et al., 2012). Among temperate agricultural crops, Schaad (1982) and Vidhyasekaran (2004) collectively listed 20 species of seedborne bacterial pathogens (26 strains). In one of the few tropical examples, Cottyn et al.

(2001) characterized bacterial communities of crushed seeds from harvested rice from farms in the Philippines. They identified a large proportion of *Pseudomonas* spp. (14 %), one of the most commonly represented genera on the phyllosphere among temperate crops as well as tropical trees (Vorholt, 2012; Bodenhausen et al., 2013; Kembel et al., 2014). More recently, Darrasse et al. (2010) demonstrated the transmission of *Xanthomonas* bean flowers from parent to offspring via seed. Bacterial species in the genus *Xanthomonas* are particularly inimical to tropical crop species (discussed below). In all, seeds in the tropics may inherit a large portion of their microbiome from the parent plant, and these communities may colonize the phyllosphere after germination. The vertical transmission of bacteria may have huge implications for plant populations as well as community dynamics if pathogenic bacteria are transferred from one generation to the next.

The Core Microbiome

A recent study demonstrated that a core microbiome (see above) occurs on the phyllosphere among 57 tree species in a tropical forest, which starkly contrasts from a similar study among 56 temperate tree species (Redford et al., 2010; Kembel et al., 2014). For adult tropical trees, bacterial OTUs (operational taxonomic units, or the taxonomic level of bacterial sampling typically binned at 97 % sequence similarity) representing only 1.4 % of bacterial diversity were present on over 90 % of all individuals and made up 73 % of the total sequences (Schloss & Westcott, 2011). Simply put, a small subset of bacteria occurred over and over among all species of trees and made up a core microbiome (sensu Shade & Handelsman, 2012; Rastogi et al., 2012). This is a surprising result and suggests that a small group of bacteria are either the best at colonizing these tree species, or the best at surviving on the phyllosphere, or a combination of both. Comparatively, Redford et al. (2010) failed to identify a core microbiome for bacterial communities on 56 temperate tree species in Colorado using similar techniques. Here, not a single OTU co-occurred on the phyllosphere of all tree species. Regardless, it remains uncertain the degree to which OTUs in the core microbiome are beneficial or harmful to host plants. Additionally, whether these communities colonize via active recruitment by plant hosts or differential survival of bacteria remains poorly explored. Nevertheless, the finding that a small fraction of bacteria repeatedly co-occur across a large number of tree species in a small area of tropical forest is important and its ecological consequences deserve immediate attention.

A key goal for future research should be to understand the degree to which various sources (e.g., wind vs. insects) contribute to the bacterial phyllosphere, particularly to help us understand plant microbe interactions and how these will likely change. Molecular techniques should be used to determine whether plant hosts actively “recruit” bacterial mutualists to the phyllosphere, as they do for bacterial mutualists in the rhizosphere (reviewed by Mendes et al., 2013). Additionally, understanding the ecology of these taxa is critical, particularly in a changing world where these interactions, as well as the drivers of these interactions, will likely change. Indeed, climate change is projected to significantly alter biogeochemical cycles (Walther et al., 2002; Laurence & Peres, 2006; Lewis et al., 2009) as well as insect herbivores (Bale et al., 2002, Dyer et al., 2012) and precipitation (Walther et al., 2002). Uncovering the contributions of soil, animal vectors, wind and rain to phyllosphere communities may enable us to predict how global climate change will alter these bacterial communities and ultimately their plant hosts.

From the Canopy to the Forest Floor: Temperature, Humidity, and Radiation Structure Phyllobacterial Communities

Temperature and Humidity

Temperature and humidity in the tropical understory may be close to optimal for the survival and persistence of a large portion of phyllosphere bacteria. In general, many plant-pathogenic bacteria experience optimal growth at high humidity and at temperatures between 25 and 30 °C (Smirnova et al., 2001). An absence of cold temperatures is also key because winter freezing in temperate zones typically kills more than 99 % of plant pathogens each year (Burdon et al., 1996). Additionally, high moisture or humidity in tropical habitats likely support more abundant bacterial communities. For example, Monier & Lindow (2004) discovered that populations of the pathogen *Pseudomonas syringae* on bean leaves in agricultural fields decreased by 99 % after 8 days under low humidity (<50 %) whereas this species increased three-fold in 100 % relative humidity after 8 days (Monier & Lindow, 2004). Moreover, high humidity may increase the infection rate of foliar bacteria. Leben (1988) found that the infection rate of *P. syringae* on cucumber leaves increased by 48 % under high humidity (80–100 %) versus low humidity (30–50 %). Taken together these results suggest that persistently warm, moist, and humid tropical habitats will allow bacteria to reach densities that are much higher and more persistent than in temperate regions where below freezing temperatures knock back populations each year.

UV Radiation

Based on studies in temperate systems, we predict that UV radiation likely stratifies phyllobacterial communities from the canopy to the forest floor in tropical forests. High radiation levels damage bacterial DNA and moreover may restrict phyllobacteria to protected sites on the leaf such at trichome bases, stomatal openings, hydathodes (structures that allow the exudation of water from leaves), and beneath or in openings in the cuticle (Corpe & Rheem, 1989; Pfeifer, 1997; reviewed by Beattie & Lindow, 1999). In addition, the relative abundance of pigmented bacteria on the phyllosphere increases as radiation increases, and these pigments allow bacteria to withstand greater UV exposure by absorbing radiation and quenching oxygen free radicals (Corpe & Rheem, 1989; Sundin & Murillo, 1999; Kim & Sundin, 2000; 2001; Jacobs et al., 2005; Gunasekera & Sundin, 2006). Poplawsky et al. (2000) discovered that survival of *X. campestris*, the most destructive pathogen attacking Brassicaceae worldwide, decreases 1000 fold in the absence of its naturally-produced xanthomonadin pigments. In general, we predict bacterial abundance and diversity in tropical forests to increase from the canopy to the forest floor where light penetration can diminish to less than 1 % (Bjorkman & Ludlow, 1972; Chazdon & Fletcher, 1984). Moreover, bacteria in high light habitats (canopy, early successional) will likely be restricted to subsets with traits that confer UV tolerance. To our knowledge, the degree to which these adaptations are costly for phyllobacteria remains unexplored.

Tropical Leaf Architecture Likely Supports Greater Phyllobacterial Colonization and Abundance Compared to Temperate Leaves

The architecture of leaves in tropical forests likely enhance abundance and diversity of phyllobacteria compared to their temperate counterparts. These traits include longer leaf life span, larger leaf surface area, lower degree of deciduousness, and higher hydathode density (Table 1). Together, these traits promote a larger and more stable substrate for bacteria to colonize or persist on and provide more microsites that afford protection. Moreover, some leaf traits that confer defense from arthropod enemies may make plant hosts more vulnerable to bacterial enemies. For instance, 30 % of vascular plants have glandular trichomes, or specialized hair tissues with glands that secrete chemicals to ward off herbivores (reviewed by Levin, 1973; Wagner, 1991; Wagner et al., 2004; Tissier, 2012). Glandular as well as non-glandular trichomes (simple hairs) can be constitutive and even induced in response to herbivore attack (Traw & Dawson, 2003; Traw, 2002; Traw & Bergelson, 2003; Shepherd et al., 2005; Gonzales et al., 2008). However, bacteria aggregate and are protected around the bases of glandular trichomes (Huang, 1986; Monier & Lindow, 2003; 2005), and in addition may benefit from secondary metabolites produced at the base of these trichomes (Karamanoli et al., 2012; but cf. Reisberg et al., 2012). If these bacteria are pathogenic, then a trait that deters herbivores may simultaneously enhance disease. This can potentially be a costly trade-off and suggests that the benefits of producing glandular trichomes must be particularly beneficial for plants if in these trichomes harbor and protect bacterial enemies.

Overall, we predict that colonization and abundance of bacteria on leaves in the tropics will be higher than in temperate zones. Out of 15 leaf traits, 11 show a sharp contrast between temperate and tropical forests (Table 1). Out of these 11 traits, seven will likely favor higher bacterial colonization, abundance, and survivorship among tropical leaves while 4 traits will favor an increase in these metrics among temperate leaves. Although simplified, we feel that these traits may be used to predict which systems, as well as which species and growth forms, will likely harbor more abundant and diverse communities of foliar bacteria. In fact, we argue that phyllobacterial communities should be classified as an independent leaf functional trait, which would classify phyllobacteria as a major axis of plant ecological strategy variation (see also Kembel et al., 2014).

Interactions Among Bacteria on the Leaf Surface

Competition and Niche Partitioning

Carbon sources required for microbial growth are often limited on the leaf surface (Bashi & Fokkema, 1977; Fokkema et al., 1979; Dik & Vanpelt, 1992; Wilson & Lindow, 1994; Mercier & Lindow, 2000). Studies to date demonstrate that phyllobacterial populations increase as carbon resources increase and epiphytic bacteria rapidly consume these resources. For example, Mercier and Lindow (2000)

Table 1 A comparison of leaf traits between temperate and tropical systems and their predicted effects on bacterial communities

Leaf Trait that improves suitability for bacteria	Temperate habitats	Tropical Habitats	Effect on foliar bacteria
Leaf lifespan	lower	higher[1, 2]	Increases time for colonization, decrease diversity [3,4,5,6, 42] but cf. [7, 46, 47] Cuticle erodes, greater wettability[43]
Lower deciduousness (wet forests)	lower	higher[2, 8]	Increases time for colonization, decrease diversity [3,4,5,6, 42] but cf. [7]
Higher degree of leaf venation	lower	higher[9]	Increases bacterial entry and movement [10]
Higher hydathode density	lower	higher[11]	Increases entry [12]
Higher SLA (evergreen wet forests)	lower	higher[13 but cf. 14]	Increases colonization [15]
Higher insect damage	lower	higher[1, 2]	Increases colonization and entry [16, 17]
Higher leaf wettability	lower	higher[18]	Increases entry [19, 20]
Lower toughness (fiber)	higher[1, 2, 21]	lower	Increases bacterial attachment and entry, increases intercellular movement [20, 22, 23, 24]
Lower chemical defenses	higher[1, 2, 25, 26]	lower	Increases abundance [27]
Higher trichome density	unknown	unknown	Increases colonization, attachment, and entry [29, 30, 31]; increases spatial heterogeneity and enhances microbial diversity[39]
Lower drip tip prevalence	lower	higher[32, 35]	Increases attachment and splash dispersal[32, 33, 34, 35]
Lower degree of cuticular waxes	lower	higher in young leaves and abaxial surface[28]	Increases attachment and entry and nutrient availability and acquisition [36, 43]
Higher stomatal density	No difference	No difference; however, lower stomatal density in understory than in canopy in tropics [40 cited in 37]	Increases entry [12] but cf. [38, 41]

Table 1 (continued)

Leaf Trait that improves suitability for bacteria	Temperate habitats	Tropical Habitats	Effect on foliar bacteria
Higher surface heterogeneity	unknown	unknown [1, 2]	Increases species coexistence [44, 45]
Higher degree of dissection	unknown	unknown	Decreases attachment and colonization [15]

Sources by corresponding numbers: (1) Coley & Aide, 1991; (2) Coley & Barone, 1996; (3) Ercolani, 1991; (4) Redford & Fierer, 2009; (5) Friesen et al., 2011; (6) Yadav et al., 2011; (7) Jackson & Denney, 2011; (8) Aerts, 1995; (9) Roth-Nebelsick et al., 2001; (10) Thorne et al., 2006; (11) Tukey, 1970; (12) Beattie & Lindow, 1999; (13) Murphy & Lugo, 1986; (14) Asner et al., 2003; (15) Delmotte et al., 2009; (16) Stavrinides et al., 2009; (17) Nadarasah & Stavrinides, 2011; (18) Aryal & Neuner, 2010; (19) Evans et al., 1992; (20) Lindow & Brandl, 2003; (21) Hallam & Read, 2006; (22) Choong et al., 1992; (23) Yadav et al., 2005; (24) Alfano & Collmer, 1996; (25) Levin, 1976; (26) Levin & York, 1978; (27) Joosten & van Veen, 2011; (28) Neinhuis & Barthlott, 1997; (29) Huang, 1986; (30) Monier & Lindow, 2003; (31) Monier & Lindow, 2005; (32) Richards, 1996; (33) Ivey & DeSilva, 2001; (34) Burd, 2007; (35) Malhado et al., 2012; (36) Marcell & Beattie, 2002; (37) Bazzaz & Pickett, 1980; (38) Melotto et al., 2006; (39) Vokou et al., 2012; (40) McLean, 1919; (41) Melotto et al., 2008; (42) Kinkel, 1997; (43) Beattie, 2002; (44) Comins & Noble, 1985; (45) Tilman, 1994; (46) Thompson et al., 1993; (47) Penuelas et al., 2012

We (1) list leaf traits that increase habitat suitability for foliar bacteria; (2) compare the prevalence of these traits between temperate and tropical systems; and (3) predict how these traits structure foliar bacteria. Here we define colonization as arrival per unit time; attachment as ability to stick to the leaf surface; and entry as the ability to gain access to internal leaf tissue. Though not a plant trait, we include damage in the table because it provides conduits for bacteria to enter leaf tissue and insects can vector bacteria among individuals quantified the total amount of mono- and polysaccharide sugars on leaves of six different temperate crop species. Next, they inoculated the leaf surface of all species with the bacterial epiphyte *Pseudomonas fluorescens*. Bacteria reached higher densities on plant species with higher sugar content. Moreover, in less than 24 h *P. fluorescens* depleted sugar levels on bean leaves by as much as 80 % (Mercier & Lindow, 2000). Experiments have also confirmed that interspecific competition among bacterial species occurred for sugars, suggesting these bacteria occupied similar resource niches (Ji & Wilson, 2002; Innerebner et al., 2011). In laboratory experiments, Innerebner et al. (2011) demonstrated that gram-negative *Sphingomonas* spp. decreased the population size of *P. syringae*, a pathogen with a similar carbon use profile, by up to 340-fold on the phyllosphere of *Arabidopsis*. Thus, we predict similar competitive interactions among phyllobacterial species in the wild but this remains speculative, especially the degree to which there is niche specialization or other processes that mediate or promote coexistence (see below).

Some epiphytic bacteria appear to specialize on distinct carbon sources (e.g., amino acids, organic acids, and carbohydrates), thereby allowing some degree of niche partitioning. In one of the only studies of its kind, Wilson and Lindow (1994) directly evaluated the relationship between species coexistence of epiphytic bacteria and their degree of ecological niche overlap. They inoculated potato leaves with five different bacterial species representing four different genera, and found that coexistence was promoted and competitive interactions mitigated when overlap in resource use was the least. Wilson and Lindow (1994) suggested bacteria could be placed within contrasting guilds (sensu Root, 1967) based solely on whether the bacteria specialized on amino acids versus organic acids versus carbohydrates. The variability of these compounds on the phyllosphere is likely to vary widely among plant species suggesting a critical basis for host specialization or affinity as well as coexistence.

Niche differentiation via habitat specialization likely occurs on the phyllosphere based upon fine scale leaf-surface heterogeneity, which is akin to the pit and mound topography that occurs on the forest floor (e.g., Putz, 1983; Peterson et al., 1990). Leaf surface landscapes are complex because of the presence of stomates, trichomes, and veins, as well as wide spatial variation in waxy cuticle layers and epiphyllous lichens in tropical systems (Mechaber et al., 1996; Lucking, 2001; Mechaber, 2002; Vorholt, 2012). In fact, Andrews (1992) noted that the distance to the top of an 800 μm trichome for a bacterium on the cuticle is four times greater than the distance from a person on the sidewalk to the top of the Sears Tower in Chicago. The extent to which phyllobacteria specialize on contrasting microhabitats isn’t clear, but recent evidence suggests that the geography of the phyllosphere appears to shape taxa-specific colonization patterns on particular microhabitats (Remus-Emsermann et al., 2012; 2014). Further, it has long been known that UV-tolerant, pigmented bacterial species occur more readily across the leaf surface while other bacteria require “nooks and crannies” that shield them from harsh environmental conditions (see reviews by Beattie & Lindow, 1999; Lindow & Brandl, 2003; reviewed by Andrews & Harris, 2000). Mechaber et al. (1996) used atomic force microscopy to document the upper leaf landscape of cranberry. They found that young leaves contained a more homogeneous regular pattern of broad expanses or plateaus while older leaves were more heterogenous where heights changed more rapidly over shorter distances. Thus, we predict that the more irregular and sharper topographical contrasts that are occur on older leaves will enhance bacterial diversity and coexistence on the phyllosphere (Ricklefs, 1977; Comins & Noble, 1985; Tilman, 1994). This also might suggest the existence of repeatable patterns of bacterial succession as leaves age (see Redford & Fierer, 2009).

Bacterial Aggregation

Highly dense patches of bacteria enable individuals to communicate and even exchange genetic material with each other, which may explain how and when bacteria become pathogenic. The crowding of bacteria allows for quorum sensing (Box 2), a process by which individuals communicate so that certain traits are expressed when bacterial density reaches a minimum threshold (reviewed by von Bodman et al., 2003). Pathogens use quorum sensing to coordinate certain behaviors such as biofilm formation and exopolysaccharide production to enhance survival (Table 2). Additionally, quorum sensing allows pathogens to mount attacks together against plant hosts by triggering certain bacterial behaviors such as the production of chemicals that may be used to breach plant cell walls (von Bodman et al., 2003). Conversely, bacterial mutualists enhance plant performance by using quorum sensing to produce plant hormones and inducing plant resistance to pathogens (discussed below; reviewed by Hartmann et al., 2014). Perhaps more importantly, aggregating bacterial cells may spur the transfer of virulence or symbiosis-related factors among each other via horizontal gene transfer (the swapping of genetic material among neighboring bacteria; Bailey et al., 1996; Ochman et al., 2000; van Elsas et al., 2003; Sorensen et al., 2005). Indeed, plasmid gene transfer among *P. putida* strains on bean leaves occurred at frequencies as high as 33 % in one experiment and as high as 40 % among *P. syringae* cells in another (Normander et al., 1998; Bjorklof et al., 2000). In all, aggregates of phyllosphere bacteria particularly among protected microsites (e.g., trichome bases, stomates, hydathodes) will likely enhance bacterial survival and increase virulence for pathogenic species.

Box 2 Quorum sensing

Bacteria can monitor their own population density through the production and release of small, diffusible signals that enable them to synchronize the expression of specialized gene systems (Waters & Bassler, 2005). This process is called quorum sensing, which simply put means that bacteria can “count” their own numbers and alter their behavior accordingly (reviewed by von Bodman et al., 2003). Thus, individual bacteria can in essence “gang up” on their hosts, which may be particularly beneficial for pathogenic bacteria that aggregate at protected sites on the leaf surface (reviewed by Beattie & Lindow, 1999). In fact, quorum sensing might even camouflage bacterial pathogen populations by preventing or delaying host plant response until density is high enough to mount a formidable attack (Abramovitch et al., 2006). Additionally, bacteria can use quorum sensing to simultaneously produce compounds that can enhance stress tolerance to heat, UV radiation, or drought (Quinones et al., 2005; see Table 2). Other compounds produced via quorum sensing increase virulence by breaking down plant cell walls or aiding motility thereby promoting infection (Whitehead et al., 2002; Shepherd & Lindow, 2009). Quorum sensing molecules have been identified among many bacterial species that commonly associate with plants (see reviews by Cha et al., 1998; Loh et al., 2002; von Bodman et al., 2003; Ahmad et al., 2008; Hartmann et al., 2014). In fact, Elasri et al. (2001) identified quorum-sensing molecules from a pool of 340 bacterial strains isolated from tissues of over 60 temperate crop species as well as in soil. They discovered that a larger portion of foliar and stem associated strains contained quorum-sensing molecules (49 %) than root-associated strains (28 %) and free-living strains from soil (0 %). Although the degree to which phyllobacteria among tropical plant hosts rely on quorum sensing to coordinate group behavior is unknown, these findings suggest that a large portion of leaf-associated bacteria rely on this phenomenon for survival and function.

Table 2 The bacterial traits associated with survival and fitness of bacterial pathogens on the phyllosphere

Trait	Bacterial species	Host species	Mode of action	Effect	Sources
Low susceptibility to desiccation	*Pseudomonas syringae, Pantoea stewartii, Xanthomonas campestris, X. axonopodis*	Bean, ivy, grand fir, walnut, cherry laurel	Exopolysacch-aride (EPS) production; biosurfactant production	Maintains hydrated level surrounding bacteria and increases survival	1–3, 30–35, reviewed by 39
Low susceptibility to UV radiation	*P. syringae, P. aeruginosa, Pantoea stewartii, X. campestris*	Bean	Pigment production	Absorbs radiation and quenches free radicals	22–27,
High motility	*P. syringae*; *Xanthomonas* spp.	Bean, In vitro	Enhanced by quorum sensing, flagellin production, "riding" other motile bacteria	Enables cells to locate resources and to gain access to protected sites	3, 4, 5, 28
Efflux pump expression	*X. oryzae, Erwinia* spp., *Pseudomonas* spp.	*Arabidopsis*, bean, in vitro	Evade plant immune system by enabling bacterial effectors safe passage into plant host cells	Plant antimicrobial compound resistance	41–47
Resistance to heat and oxidative stress	*P. syringae*	Bean	EPS (aliginate) production	Reduces susceptibility to reactive oxygen intermediates	1–3, 6
Coenzyme production	*P. aeruginosa, Erwinia carotovora* (now *Pectobacterium carotovorum*)	*Arabidopsis*, corn	Facilitates quorum sensing	Increases ability to macerate plant tissue	7–10, 36
Virulence	*P. syringae,* *P. stewartii*	Bean, sweet corn, maize	Controlled by *vir* genes	Enables rapid invasion of internal leaf tissue; causes more host disease symptoms and dehydration	3, 11
Bacterial cell adhesion	*P. stewartii*	In vitro	Docking an locking through a series of physiochemical interactions	Enhances biofilm formation	11, 37
Biofilm formation	*P. stewartii,* *P. syringae, Xylella fastidiosa, Clavibacter michiganensis, X. campestris*	Corn; grape vine; potato	After initial colonization on surface, controlled via quorum sensing, cell division, and recruitment	Enhances microbial resistance to antibiotic compounds, enhances communication among cells	Reviewed by 12–15, 21, 29, 40

Table 2 (continued)

Trait	Bacterial species	Host species	Mode of action	Effect	Sources
Ability to transfer DNA	*Agrobacterium tumefaciens*	In vitro, used for GMOs of alfalfa, corn, cotton, creeping bentgrass, rapeseed, rice, soybean, sugar beet, wheat	Conjugation system controlled by quorum sensing that transfers plasmids from donor to recipient via a complex secretion system	Allows cells to obtain tumor-inducing plasmids	16–18, reviewed by 19; 20

Sources by corresponding numbers: (1) Leigh & Coplin, 1992; (2) Ophir & Gutnick, 1994; (3) Quinones et al., 2005; (4) Haefele & Lindow, 1987; (5) Lindow et al., 1993; (6) Keith & Bender, 1999; (7) Jones et al., 1993; (8) Rahme et al., 2000; (9) Whitehead et al., 2002; (10) Von Bodman et al., 2003; (11) Koutsoudis et al., 2006; (12) Watnick & Kolter, 2000; (13) O'Toole et al., 2000; (14) Morris & Monier, 2003; (15) Flemming & Wingender, 2010; (16) Piper et al., 1993; (17) Ellis et al., 1982; (18) Zhang et al., 1993; (19) Pitzschke & Hirt, 2010; (20) FDA, 2013; (21) Mann & Wozniak, 2012; (22) Corpe & Rheem, 1989; (23) Sundin & Murillo, 1999; (24) Kim & Sundin, 2000; (25) Kim & Sundin, 2000; (26) Jacobs et al., 2005; (27) Gunasekera & Sundin, 2006; (28) Hagai et al., 2014; (29) Mah & O'Toole, 2001; (30) Schreiber, 1996; (31) Knoll & Schreiber, 1998; (32) Knoll & Schreiber, 2000; (33) Schreiber et al., 2005; (34) Chang et al., 2007; (35) Rigano et al., 2007; (36) Dong et al., 2000; (37) Dunne, 2002; (38) Danhorn & Fuqua, 2007; (39) Beattie, 2011; (40) Rudrappa et al., 2008; (41) Goel et al., 2002; (42) Burse et al., 2004a; (43) Burse et al., 2004b; (44) Kang & Gross, 2005; (45) Maggiorani Valecillos et al., 2006; (46) Stoitsova et al., 2008; (47) Fan et al., 2011

We list the traits that enhance pathogen survival, pathogen identity, and whether the strains resided on plant host leaves, or if studies were conducted in vitro. Additionally, we note the mechanisms involved for each trait as well as the effect of these traits on pathogen survival and persistence

Bacterial-Fungal Interactions on the Phyllosphere

Bacteria can dramatically reduce fungal pathogen disease severity on the phyllosphere (see Table 3), and this may be particularly important in controlling fungal pathogens in tropical agroecosystems. For example, in Colombia, the fungal pathogen *Mycosphaerella fijiensis* causes the black sigatoka leaf spot disease in banana plantations that reduce banana yields by nearly 40 % over vast regions pantropically (Marin et al., 2003). Ceballos et al. (2012) recently discovered that two widespread bacterial epiphytes, gram-positive *Bacillus subtilis* and *B. amyloliquefaciens*, isolated from banana leaves in Colombia caused dramatic reductions (>90 %) of black sigatoka (Ceballos et al., 2012) by interfering with fungal hyphae formation and inhibiting the germination of ascospores. The ability of these bacteria to form microbial biofilms appeared necessary for these bacteria to suppress the fungus. These results, though narrow and simplified in scope, suggest that bacteria may commonly mitigate or mediate fungal pathogens in natural systems. This area is ripe for additional research.

There are a few documented cases where phyllobacteria induce systemic host resistance to the entire plant from attack by fungal pathogens and other enemies (Bargabus et al., 2002; 2004; Tran et al., 2007; Verhagen et al., 2010; Brotman et al., 2012; Desoignies et al., 2013). This is similar to when exposure to a fungal pathogen triggers induced systemic host resistance; however, here the bacteria act as an early warning system and “alert” their host plants to the presence of pathogenic fungi (van Loon et al., 1998; Pieterse et al., 1998). This mutualism appears common for rhizosphere bacteria and confers plant resistance to soil pathogens, nematodes, and insects (van Loon et al., 1998; van Loon & Bakker, 2006; van Wees et al., 2008; Pineda et al., 2010). Unfortunately the degree to which phyllosphere bacteria are mutualists and suppress disease in situ is poorly understood. However, when they do, Jacobsen (2006) argued that these bacteria would benefit plant hosts most likely by triggering systemic resistance. In greenhouse and field experiments on sugar beet leaves, Bargabus et al. (2002, 2004) demonstrated that nonpathogenic bacteria (*P. fluorescens*, *Bacillus mycoides* and *B. pumilus*, respectively) produced compounds to induce resistance to pathogenic fungi (*Heterodera schachtii* and *Cercospora beticola*, respectively), thereby reducing fungal abundance by up to 90 %. Similarly, Tran et al. (2007) and Desoignies et al. (2013) found that non-pathogenic bacteria could also significantly suppress fungal pathogens in the laboratory on both tomato and beet leaves. Further, *Pseudomonas* spp., many of which reside in one of the most abundant genera in phyllosphere communities among agricultural crops as well as tropical trees, commonly induce systemic resistance to fungal infection (reviewed by Jankiewicz & Koltonowicz, 2012; Vorholt, 2012, Kembel et al., 2014). These findings are important because fungal pathogens are major agents of mortality for numerous species of tropical tree seedlings, particularly those in shaded understories (Augspurger, 1984; Augspurger & Kelly, 1984; Wenny, 2000). Though induced systemic host resistance may be common in the wild, to our knowledge the degree to which phyllobacterial mutualists induce enemy resistance for plant hosts has never been evaluated outside of an agricultural context.

Table 3 A review of bacterial strains that significantly reduce the severity of fungal and oomycete pathogens on the phyllosphere

Plant Host	Bacterium	Location	Pathogen	Origin of biocontrol strain	Proposed mechanism	Sources
Alfalfa	*Bacillus cereus*	In vitro and in vivo, in laboratory	*Phytophthora medicaginis*	Cultured, but strain source not specified	Antibiosis	1
Rice	*Bacillus megaterium*, *Aspergillus niger*	In vitro and in vivo, in laboratory and in field	*Rhizoctonia solani*	Isolated strains from the field	Not determined	2
Cacao	*Bacillus* spp. (endophytes)	In vitro and in vivo, in laboratory and in greenhouse	*Phytophthora capsici*, *Moniliophthora roreri*, *M. perniciosa*	Isolates from sugar beet, tomato, and potato; endophytes isolated from cacao in Ecuador	Competitive exclusion, suggestive of induced systemic resistance	3, 4
Banana	*Bacillus subtilis*, *B. amyloliquefaciens*	In vitro in laboratory	*Mycosphaerella fijiensis*	Isolated from crops in Colombia	>80 % inhibition of ascospore germination, hydrolytic enzyme production	5, 12
Black mangrove	*B. amyloliquefaciens* (endophytes)	In vitro, in pots and in field in China	*Ralstonia solanacearum*	Isolated from mangrove leaves	Antimicrobial substances	6
Chickpea	*B. cereus*	In laboratory and in field in India	*Botrytis cinera*	Isolated from chickpea rhizosphere in India	Inhibited fungal germination, lysed conidia	15
Groundnut	*B. circulans/ Serratia marcescens* (+ colloidal chitin)	In vitro in the laboratory, In vivo in greenhouse and in the field in India	*Phaeoisariopsis personata*	Selected from collection of peanut-associated strains	Inhibited fungal germination, lysed conidia, activating defense enzymes	13, 14
Grapevine	*Pseudomonas* spp.	In vitro in laboratory	*B. cinerea*	Cultured from rhizosphere	Elicits host systemic resistance	16
Sugar Beet	*Bacillus mycoides*, *Bacillus pumilis*	In vitro and in vivo in glasshouse and in the field	*Cercospora beticola*	Isolated from sugar beet leaves in Montana	Elicits host systemic resistance to pathogen	7, 8
Tomato	*Bacillus* spp., *Pantoea* spp.	In vivo in greenhouse and field conditions	*B. cinerea, Fulvia fulva, Alternaria solani*	Randomly selected bacterial strains	Plant hormone production, quorum sensing capabilities	9

Table 3 (continued)

Plant Host	Bacterium	Location	Pathogen	Origin of biocontrol strain	Proposed mechanism	Sources
Centella asiatica	*Bacillus subtilis, Pseudomonas fluorescens* (endophytes)	In vitro, in vivo with plants in laboratory	*Colletotrichum*	Isolated from inside *Centella* leaves from Madagascar	Allelochem-icals, induced plant defense	10
Various crops, primarily tomato, grape vine, strawberry	*Bacillus* spp., *Pantoea* spp. *Pseudomonas* spp., *Bacillus* spp.	In vitro and in vivo, greenhouse and field conditions	*B. cinera*	Review	Competition, antibiosis	11
Cucumber	*B. mycodies, B. mojavensis*	In vivo in greenhouse	*Glomerella cingulate*	Isolated from sugar beet leaves; sugar beet seed emryos	Induced systemic acquired resistance	17

Sources by corresponding numbers: (1) Silo-Suh et al., 1994; (2) De Costa et al., 2008; (3) Melnick et al., 2008; (4) Melnick et al., 2011; (5) Ceballos et al., 2012; (6) Hu et al., 2010; (7) Bargabus et al., 2002; (8) Bargabus et al., 2004; (9) Enya et al., 2007; (10) Rakotoniriana et al., 2013; (11) Elad, 1996; (12) Collins & Jacobsen, 2003; (13) Kishore et al., 2005a; (14) Kishore et al., 2005b; (15) Kishore & Pande, 2006; (16) Verhagen et al., 2010; (17) Neher et al., 2009

While bacteria have been characterized as biocontrol agents against other pathogens on crop fruits and other tissues (reviewed by Janisiewicz & Korsten, 2002; Sharma et al., 2009), here we exclusively focus on the phyllosphere. We list the mutualistic bacterial strains and the pathogenic strains they excluded, as well as the plant host, and whether the studies were conducted in vitro (i.e., petri dishes) or in vivo (in plants), and in the laboratory, greenhouse, or in the field. Last, we note the proposed mechanism for pathogen reduction

Bacteria in the Interior Portions of Plant Tissue and Their Impacts on Plant Performance

Gaining Access to the Interior of the Leaf

Phyllobacteria use multiple pathways to gain access into the leaf interior where they can then act as mutualists or pathogens. Phyllobacteria enter leaves at leaf openings such as trichome bases, stomata, or hydathodes (reviewed by Beattie & Lindow, 1995), or wounds created by insects (Agrios, 2005). Additionally, some insects passively disseminate bacteria onto or into preferred plant hosts (see above). Pathogenic bacteria also gain access to leaf interiors with extracellular virulence factors (see Box 3). For example, *P. syringae* produces coronatine, a jasmonic acid mimic that suppresses the tomato defense to pathogens and induces stomatal opening thereby allowing access to the apoplast (Zhao et al., 2003; Melotto et al., 2006; 2008). More recently, Schellenberg et al. (2010) discovered that *P. syringae* produces syringolin to open stomates on bean and *Arabidopsis* leaves. Once in the apoplast, bacteria typically have much higher growth rates (reviewed by Beattie & Lindow, 1999) where they can act as mutualistic endophytes or become pathogenic. Yu et al. (2013) recently found that once inside the apoplast of bean leaves, the pathogen *P. syringae* alters its gene expression from genes that code for exploration to those that produce enzymes and phytotoxins. This suggests that after entry, pathogens can rapidly switch patterns of resource allocation from exploration and persistence to evading the plant immune system (see Box 3).

Box 3 Bacterial pathogens and the plant immune system: an evolutionary arms race

Plants have evolved two main lines of defense to detect bacterial pathogens, and pathogens have developed mechanisms to manipulate defense responses by secreting virulence effector molecules. The first line of plant defense is called the PAMP-triggered immunity (PTI), where plant extracellular pattern recognition receptors (PPRs) attempt to identify pathogen-associated molecular patterns (PAMPs; reviewed by Dangl et al., 2013; Newman et al., 2013). Bacterial pathogens use one of six highly evolved secretion systems, most commonly types III and IV, to interfere with PTI by delivering effector proteins into plant cells (reviewed in Wooldridge, 2009). These effector proteins either inhibit plant cellular functions or mimic plant hormones (discussed in "Foliar Pathogens" section). In Type IV secretion, pathogens use conjugation to deliver effector molecules into host cells (reviewed by Zechner et al., 2012; Christie et al., 2014; Low et al., 2014). *Agrobacterium tumefaciens*, for example, uses type IV secretion to induce tumors in many agricultural crop species (reviewed by Pitzschke & Hirt, 2010). The foremost system for pathogens, though, is the type III secretion system (reviewed by Jones & Dangl, 2006). Here, bacteria use a flagellar body like a syringe to inject a conglomerate of 20–30 proteins directly into the plant tissue cells (see recent reviews by Izore et al., 2011; Buttner, 2012). Some of the most ubiquitous and deleterious bacterial pathogens, such as *P. syringae*, *Erwinia amylovora*, *Ralstonia solanacearum*, and *Xanthomonas* spp., use the Type III secretion system (Buttner, 2012).

If bacterial pathogens successfully enter the host cell, they meet the plant's highly specialized second line of defense called effector-triggered immunity (ETI, formerly known as gene-for-gene resistance; reviewed by Jones & Dangl, 2006). Plant ETI hinges on pathogen recognition by a class of receptor proteins that contain nucleotide-binding (NB) and leucine-rich repeat (LRR) domains. It is here where pathogens are "specifically recognized" by plant receptors, upon which the plant can resist disease and launch a hypersensitive response (HR, see "Foliar Pathogens.") This step in particular has led to co-evolutionary dynamics between bacteria and plant hosts, where pathogen effectors and plant receptors are notably diverse, variable, and frequently change (Boller & He, 2009; Dodds & Rathjen, 2010). While successful pathogen detection results in various defense responses, a successful pathogen suppresses or evades detection and is thereby able to cause disease.

Bacterial Endophytes Significantly Promote Plant Growth: Lessons from Root Endophytes

Much of what we know about the ecology of bacterial endophytes comes from root-associated bacteria (see reviews by Anand et al., 2006; Hardoim et al., 2008; Berg, 2009; Compant et al., 2010; Berg et al., 2014). Bacterial endophytes in roots protect plant hosts from pathogens and pests. Like epiphytes, endophytes colonize an ecological niche similar to phytopathogens and may simply compete for similar niches or carbon resources, thereby reducing the abundance of bacterial pathogens (Hallmann et al., 1997). For example, up to 35 % of root-associated bacteria inhibit fungal pathogen growth in vitro (e.g., Berg et al., 2002; 2005; Berg & Hallmann, 2006). Additionally, root bacterial endophytes may induce plant host systemic resistance to pathogens (discussed above), which can significantly decrease the severity of bacterial or fungal pathogens. Further, root endophytes produce or alter plant hormonal levels to enhance plant growth (see reviews by Rosenblueth & Martinez-Romero, 2006; Kloepper & Ryu, 2006; Hardoim et al., 2008). For example, root endophytes produce the plant growth regulator auxin, which controls root and meristem cell elongation and aid in regenerating wounded tissues (Davies, 1995, Schmelz et al., 2003; Spaepen et al., 2007; but cf Silverstone et al., 1993; Brandl & Lindow, 1998). In fact, more than 80 % of bacteria in the rhizosphere produce auxins, however the prevalence of this among foliar endophytes remains unexplored (Ramos-Solano et al., 2008; but cf Hoffman et al., 2013 for endohyphal bacteria). Additionally, root endophytes produce gibberellin (Gutierrez-Manero et al., 2001) and cytokinins (Bhore et al., 2010), which control diverse aspects of plant growth and development including root and stem elongation, leaf expansion, and senescence (reviewed by Santer et al., 2009). Root endophytes also break down the plant hormone ethylene via ACC deaminase to alleviate its adverse effects on plant growth (Glick, 2005; Saleem et al., 2007). Though we recognize that conditions in the rhizosphere and phyllosphere are different in many ways (e.g., different stressors, O_2 levels, moisture regimes, etc.) and make direct comparisons somewhat tricky, we ultimately predict that foliar endophytes in the wild likely use similar mechanisms to enhance plant performance.

Additionally, bacterial endophytes isolated from all plant tissues including leaves inhibit fungal pathogens by synthesizing antifungal compounds (reviewed by Strobel et al., 2004; Brader et al., 2014). For example, *Pseudomonas* spp. comprise one of the most common and ubiquitous genera of bacterial endophytes and produce a group of antifungal peptides called pseudomycins (Strobel et al., 2004; Berdy, 2005). These peptides decrease the fungal pathogens that cause Dutch elm disease (*Ceratocystis ulmi*) and banana's black Sigatoka (*Mycosphaerella fijiensis*; Harrison et al., 1991; Ballio et al., 1994). While all of the above work was done in vitro, we predict that foliar endophytes in the wild may synthesize antifungal properties to ward off pathogens in leaves and suggest that this should be a research priority.

Foliar Pathogens: Who they are, how they Overcome Plant Defenses, and Their Deleterious Potential to Tropical Plants

The Main Players

Over 100 species of foliar bacteria are pathogenic and once in the apoplast cause hundreds of diseases to crops worldwide, though none are more "scientifically and economically important" than *Pseudomonas syringae* (Jackson, 2009; Mansfield et al., 2012). Pathogens may either be necrotrophs that first destroy host cells and later feed on the contents or biotrophs that derive nutrients from host cells without killing them (Glazebrook, 2005). Many bacterial pathogens, including *P. syringae*, display both lifestyles (Glazebrook, 2005). *P. syringae* is by far the most extensively studied and possibly the most ubiquitous foliar pathogen in the world (Morris et al., 2013). At least 57 pathovars (strains or set of strains) of *P. syringae* exist, which are often highly specialized to particular host species (Bull et al., 2010; Hirano & Upper, 2000; Lindeberg et al., 2012). Further *P. syringae* strains inhabit a variety of environments and interact with a wide range of plants in most regions of the world (Silby et al., 2011). *P. syringae* causes disease in the families Sapinadaceae, Amaranthaceae, Meliaceae, Rosaceae, Fabaceae, and Actinidaceae (Horst, 1990; Sarkar & Guttman, 2004). All of these families are well represented in the tropics, particularly Fabaceae (the third largest angiosperm family), whose woody species are mostly confined to tropical and subtropical habitats (Rundel, 1989).

Xanthomonas is a prominent and largely pathogenic bacterial genus whose members commonly plague tropical crop systems. *Xanthomonas* comprises almost 30 species, which typically have mixed biotrophic-necrotrophic lifestyles and collectively cause disease in nearly 400 plant species (Ryan et al., 2011). Three *Xanthomonas* species (*X. oryzae*, *X. campestris*, and *X. axonopodis*) afflict pantropical hosts and are among the top ten most "scientifically and economically important" plant pathogenic bacteria in the world (Mansfield et al., 2012). 18 sequenced *Xanthomonas* genomes have been described, 12 of which cause disease among tropical crop species, including sugarcane, banana, cassava, citrus crops, and rice (Ryan et al., 2011). These species cause major crop losses. For example, in just 3 years *X. campetris* caused a decrease in Ugandan banana and plantain yields by 30–52 % (Karamura et al., 2006). This pathogen is expected to spread throughout East and Central Africa at a rate of 8 % per year in banana plantations (Kayobyo et al., 2005; Abele & Pillay, 2007). In a 50 ha tropical forest in Panama, Kembel et al. (2014) found that Xanthomonadaceae is one of the most common families on the phyllosphere and xanthomonads alone made up almost 9 % of the core microbiome. If these bacteria are pathogenic and tree host species are differentially vulnerable, then these pathogens may be major agents of forest turnover particularly in small size classes and in areas around parent trees.

How Pathogens Overcome Plant Defenses

After entering the leaf, pathogens attempt to suppress the complex plant immune system. Pathogens inject effector proteins into plant cells, which help in evading the plant's first line of defense (Box 3) and aid in nutrient acquisition and dispersal (reviewed by Dodds & Rathjen, 2010). During the second line of defense (Box 3), plants use the jasmonic acid (JA) and salicylic acid (SA) hormone pathways to activate defenses to necrotrophs and biotrophs, respectively (Glazebrook, 2005). These two pathways are mutually inhibitory, and certain bacterial pathogens exploit this negative crosstalk to evade detection (Traw et al., 2004; Cipollini et al., 2004; reviewed by Thaler et al., 2012). For example, *P. syringae* produces jasmonic acid mimics to suppress the salicylic-acid-mediated defense in plant hosts (Zheng et al., 2012). These interactions frequently culminate in the induction of a hypersensitive response (HR) from plant hosts, which involves deliberate cell suicide localized at the infection site to limit pathogen spread (reviewed by Lam et al., 2001; Coll et al., 2011). Successful pathogens develop effectors to evade the plant's last line of defense and invade host cells to cause disease.

Bacterial Pathogens in Tropical Systems

Pathogens are particularly detrimental to tropical crops where disease losses may be 50 to 100 % higher than in temperate systems, though it remains uncertain the degree to which bacterial pathogens are inimical in hyper-diverse tropical forests (Hill & Waller, 1982; Thurston, 1998). Because the tropics are ideal for bacterial survival and persistence (see above), bacterial pathogens are likely to be more abundant and damaging. In fact, Wellman (1968, 1972) documented the known diseases (fungal and bacterial) among crops with ranges in both temperate and tropical zones. He concluded that for every disease that infected a given crop in temperate areas, there were 10 in the tropics (see also Gilbert, 2005). Clearly, a new focus on tropical bacteria is needed because papers studying pathogens in temperate systems have outnumbered tropical studies by over 25:1 (Lodge et al., 1996).

Foliar Bacteria in the Tropics

Phyllobacteria in Tropical Habitats

Phyllobacteria in the tropics are diverse, significantly contribute to forest nutrient cycling, and are likely fairly host-specific (Abril et al., 2005; Fürnkranz et al., 2008; Kembel et al., 2014). To our knowledge, Lambais et al. (2006) were the first to use culture-independent methods to identify phyllosphere bacteria of tree species in the tropics. They identified up to 671 bacterial OTUs on each of nine phylogenetically diverse canopy tree species, and estimated that the phyllosphere of Brazilian Atlantic forest alone harbors as many as 10 million bacterial OTUs. Clone libraries generated for three of these tree species (*Trichilia catigua*, *T. clausenni*, and *Campomanesia xanthocarpa*) suggested that some of these phyllobacterial taxa may, to some degree, be host-specific. For example, Proteobacteria were twice as common on the phyllosphere of *Trichilia* spp. versus *C. xanthocarpa*. Further, cyanobacteria made up almost 15 % of the total sequences on *C. xanthocarpa*, however there was not a single cyanobacterial sequence found on either *Trichilia* species. Fürnkranz et al. (2008) quantified nitrogen-fixation among phyllosphere bacteria of 13 herb, shrub, and tree species in a lowland Costa Rican forest. The bacteria associated with three of these plant species (*G. cauliflora*, *P. wendlandii*, and *C. drudei*) fixed up to 6 μmol of N_2 per m^2 per day, enough to provide significant nitrogen input to the forest. Although the bacterial communities did not differ on the two high nitrogen fixing plant species (*G. cauliflora* and *C. drudei*) versus the low one (*C. laevis*), nitrogen fixation was highly variable among the 13 plant species sampled. Though preliminary, these data suggest that bacterial communities may fix very different amounts of nitrogen depending on the host. Further, nitrogen fixation by foliar bacteria may be patchy among tropical plants because they occur on host species that may be wildly scattered across the landscape.

Evidence from two recent studies suggests that host phylogenetic relationships are critical for structuring bacterial communities on the phyllosphere of tropical trees. Kim et al. (2012) characterized bacterial communities on leaves of six tree species in an arboretum in Malaysia. The relative abundance of bacterial taxa differed significantly among tree species. These differences were particularly prominent for Gammaproteobacteria, which is the second most common bacterial phylum among tree species in Panama (Kembel et al., 2014). More recently, Kembel et al. (2014) quantified bacterial communities on the phyllosphere of 57 mid-canopy tree species in a moist tropical forest. Bacterial taxa exhibited high host affinity, with plant host taxonomy explaining 47 % of the variation of bacterial communities. A suite of plant host traits dealing primarily with growth and mortality rates, nutrient concentrations, and leaf characteristics was also important in explaining variation (26 %) among bacterial communities. Overall, these findings suggest that bacterial communities on the phyllosphere of tropical trees are associated with particular plant hosts and are structured by key plant traits.

Bacterial Endophytes in Tropical Habitats

Though a handful of studies have characterized foliar bacterial endophytes among tropical trees, few generalizations are possible about these bacterial communities or their ecology. Bacterial endophytes have been studied primarily among crop species and have only been characterized in a few gymnosperm and angiosperm species (see reviews from Hallmann et al., 1997; Hardoim et al., 2008; Berg, 2009; Compant et al., 2010; Izumi, 2011; Carrell & Frank, 2014). Coffee, cacao, *Citrus*, and *Eucalyptus*, and black mangroves are the only tropical trees for which foliar endophytes have been characterized (Araujo et al., 2002; Vega et al., 2005; Shiomi et al., 2006; Hu et al., 2010; Melnick et al., 2011; Paz et al., 2012; for fungal endophytes in cacao leaves, see Herre et al., 2007, Mejía et al., 2008; 2014). The endophytic strains isolated were predominantly *Bacillus* spp. in all studies, and the authors suggested these strains could be used as biocontrol agents against fungal as well as bacterial diseases. In a recent study using plant stems, Bascom-Slack et al. (2009) isolated 14 endophytic actinomycete bacterial species from 12 shrub and tree species from 10 plant families in a Peruvian rainforest. Because these studies relied solely on culture dependent methods that fail to detect as much as 99 % of resident bacteria (reviewed by Müller & Ruppel, 2014, but cf Stiefel et al., 2013), it is difficult to draw conclusions about bacterial endophytic communities in tropical systems. With the exception of these few studies, the identity and ecology of foliar endophyte communities among tree hosts remain poorly explored globally. Bacterial endophytes have not been characterized from a single tree among some of the most common plant genera in the world, including *Abies*, *Acacia*, *Alnus*, *Carpinus*, *Fagus*, *Fraxinus*, and *Shorea*, many of whose species have tropical distributions (Izumi, 2011). This should be a research priority because Strobel (2012) argued that every plant on earth hosts both bacterial and fungal endophytes. Without knowing which bacteria species are present and in what abundance, it is impossible to understand anything about their impact on their hosts let alone anything about their function in the ecosystem.

A subset of gram-negative *Burkholderia* spp. reside in leaf galls of tropical angiosperms and act as lifelong obligate endosymbionts to plant hosts (reviewed by Compant et al., 2008). Unlike endophytes that colonize internal leaf tissue between mesophyll cells (Stone et al., 2000), *Burkholderia* colonize intracellularly and are surrounded by a host membrane (Reinhold-Hurek & Hurek, 2011). This association occurs in about 500 species in the families Primulaceae and Rubiaceae, particularly in the genera *Pavetta*, *Sericanthe*, and *Psychotria* of the Rubiaceae family (Miller, 1990). Despite the predominantly pantropical distribution of both families, leaf nodulated plants are restricted to tropical parts of Asia and Africa (Miller, 1990). Because *Psychotria* plants grown without *Burkholderia* resulted in distorted leaves, stunted growth, and eventual death of plant hosts (Gordon, 1963), van Oevelen et al. (2003) suggested that these two organisms have an obligate association with one another. Recently, Carlier and Eberl (2012) sequenced the genome of *Burkholderia kirkii* and discovered a collection of genes responsible for secondary metabolite synthesis on the *B. kirkii* plasmid. They hypothesized that these bacteria produce compounds to ward off pathogens and herbivores, however future studies are needed to test this hypothesis.

What are the Impacts of Bacterial Pathogens for Plant Communities in Tropical Habitats: Two Perspectives

One on hand, the detrimental impact of foliar bacterial pathogens may increase as the abundance of single host tree species increases, which can promote and maintain plant diversity in the tropics (Gillett, 1962; Janzen, 1970; Connell, 1971). Frequency-dependent reduction of conspecifics is the cornerstone for the Janzen-Connell hypothesis, which hypothesizes that density-dependent enemies regulate plant populations (Janzen, 1970; Connell, 1971; reviewed by Carson et al., 2008). This phenomenon occurs via specialist pests, who cause a reduction in the competitive ability of key plant species and make room for other plant species (Janzen, 1970; Connell, 1971). Frequency- dependent tree mortality has been observed numerous times in the tropics (most recently by Bagchi et al., 2014; see reviews by Carson et al., 2008; Mordecai, 2011; Comita et al., 2014), though not a single study determined whether this pattern exists for foliar bacteria. Griffin et al. (unpublished data) found that seedlings of three of five tree species grew 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. In addition, studies to date indicate that prominent foliar pathogens in agroecosystems are relatively host specific (e.g., Leyns et al., 1984; Ryan et al., 2011; Lindeberg et al., 2012; see above). Moreover, wind, rain and insects all spread pathogens to new hosts (Butterworth & McCartney, 1991; Pruvost et al., 2002; Bock et al., 2005; Nadarasah & Stavrinides, 2011), suggesting that conspecific aggregations of tree species will facilitate bacterial colonization among nearby conspecifics. If this is true, the implications for the maintenance of species diversity in tropical forests are clear: enemies will build up around conspecifics and reduce their performance and dominance.

Conversely, bacterial pathogens may not be host specific "enough" and therefore not act to maintain plant community diversity in tropical forests. It's possible that the degree to which foliar pathogens specialize to plant hosts in the tropics is less than in temperate systems. Kembel et al. (2014) found that a large portion of bacterial communities co-occur among 57 tree species in a tropical forest, though they did not determine whether or not these bacteria were pathogens. If these bacteria are generalists, they may simply spillover to other plant species in close proximity (Dobson, 2004, Power & Mitchell, 2004). Second, foliar pathogens in the tropics may be widespread and cause disease for plants quite broadly. For example, Morris et al. (2008) hypothesized that the dispersal of the bacterial pathogen *P. syringae* is widespread, which increases the pathogen's exposure to reservoir plant species and other susceptible plant species (Brown & Hovmoller, 2002; Keesing et al., 2006; Morris et al., 2008). Additionally, highly competitive or common species may be tolerant of a bacterial pathogen, thus causing the pathogen to spillover and harm less common or rare species (Dobson, 2004; Power & Mitchell, 2004). Pathogen spillover may cause positive feedbacks and lead to single-species dominance as the exposure to susceptible plant species increases as tolerant species become more abundant in a community (reviewed by Mordecai, 2011).

It is clear that we cannot resolve this question at this time because no studies have measured the ability of foliar pathogens to enhance or reduce plant diversity. Studies to date suggest that fungal endophytes (Arnold et al., 2003; Arnold, 2008) and insect herbivores (Dyer et al., 2007) are host specific in tropical forests, though this topic remains contentious (Cannon & Simmons, 2002; Suryanarayanan et al., 2002; Novotny et al., 2002; Novotny & Basset, 2005; Novotny et al., 2006). Though the jury is still out, particularly for foliar bacteria, we predict that bacterial pathogens will turn out to be host specific enough and thus play an important role in the maintenance of hyper-diversity in tropical forests.

Conclusions and Future Directions

Our goal was to review the "the great unseen majority" of the plant phyllosphere in tropical habitats. First, we conclude that soil, wind, water, and animal vectors (especially invertebrates) are critical in transporting bacteria to the leaf. Recent studies suggest that bacteria may disperse worldwide via global climate cycles and animal vectors; thus, bacterial dispersal is likely much greater than previously thought (Morris et al., 2008, Chapman et al., 2015).

Additionally, we argue that colonization and abundance of bacteria on leaves in the tropics will be higher than in temperate zones. Leaf architecture and environmental conditions in the tropics, particularly high year-round temperatures, all favor bacterial colonization and survival compared to their temperate counterparts. Competitive exclusion and niche differentiation among phyllospheric bacteria are based upon limiting carbon resources, and species coexistence likely occurs via niche differentiation based on carbon usage and habitat specialization. Such studies demonstrate that that the phyllosphere is likely an ideal system to test other concepts of ecological theory such as patch dynamics, island biogeography, species-area relationships, and trophic dynamics (Meyer & Leveau, 2012). Though the degree to which phyllobacteria and endophytes of tropical plants are pathogenic or mutualistic remains unknown, we predict that the bacteria are primarily pathogenic and associate with particular host species. Ultimately, we hypothesize that the detrimental impact of bacterial pathogens increases with the abundance of hosts, which can promote and maintain plant diversity in tropical forests.

The recent development of new molecular techniques will lead to novel phylogenetic and functional insight of foliar bacterial communities. Researchers recently published the first phyllospheric metagenomes, −proteomes, and –transcriptomes for crop and model plant species under agricultural and natural conditions (Delmotte et al., 2009: soybean, clover, and *Arabidopsis*; Knief et al., 2012: *Arabidopsis* and *Medicago truncatula*; Bodenhausen et al., 2013; 2014; Horton et al., 2014: *Arabidopsis*). Delmotte et al. (2009) found that on average over 30 % of proteins identified on the phyllosphere on soybean, clover, and *Arabidopsis* had never been previously described. Horton et al. (2014) recently found evidence via pyrosequencing and genome-wide associations (GWAS) to suggest that bacterial richness and community composition differ among genotypes of *Arabidopsis thaliana* (see also Bodenhausen et al., 2014). Additionally, we can begin to gain new insights on tritrophic interactions among plants, bacteria, and fungi. The “omics” approaches enable us to explore species interactions, communication, development, and diversity, and even reveal the contribution of each partner to these interactions. This will be critical for our understanding of community ecology on the phyllosphere, where plants, bacterial, and fungal communities interact (sensu Bonfante & Anca, 2009 for tritrophic interactions in the rhizosphere). Additionally, future studies should include systematic assessments of bacterial and fungal community members that simultaneously sample the rhizosphere, root endosphere, the phyllosphere and inside the leaf on the same plant host. Ultimately, the increasing pace and cost effectiveness of molecular technology development will lead to a much better understanding of the composition, physiology, and ecology of leaf bacterial communities.

Acknowledgments We thank Joe Wright, Bert Leigh, Carolin Frank, Shannon Nix, Mike Chips, Sarah Neihaus, Camilo Zalamea, Carolina Sarmiento, the Carson-Pruitt Lab Group, three anonymous reviewers, and in particular Brian Traw and Betsy Arnold for comments on various drafts of this manuscript. We thank Felipe Lacayo for translating the abstract into Spanish. We acknowledge financial support from a National Science Foundation Graduate Research Fellowship, a Smithsonian Tropical Research Institute Predoctoral Fellowship, a Lewis and Clarke Fund for Exploration and Field Research, Sigma Xi Grant-in-Aid of Research, and a CRDF grant from the University of Pittsburgh.

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Appendix

Table 4 The scientific names associated with common names of plant species used in this manuscript

Common name	Scientific name
Alfalfa	*Medicago sativa*
Banana and plantain	*Musa* spp.
Bean	*Phaseolus vulgaris*
Cacao	*Theobroma cacao*
Cassava	*Manihot esculenta*
Cherry laurel	*Prunus laurocerasus*
Citrus	*Citrus* spp.
Clover	*Trifolium* spp.
Coffee	*Coffea* spp.
Cotton	*Gossypium hirsutum*
Cranberry	*Vaccinium macrocarpon*
Creeping bentgrass	*Agrostis stolonifera*
Cucumber	*Cucumis sativus*
Grand fir	*Albies grandis*
Grape vine	*Vitis* spp.
Grapefruit	*Citrus * paradisi*
Groundnut	*Arachis hypogaea*
Ivy	*Hedera helix*
Black mangrove	*Bruguiera gymnorrhiza*
Norway spruce	*Picea abies* L. Karst
Potato	*Solanum tuberosum*
Rapeseed	*Brassica napus*
Rice	*Oryza* spp.
Soybean	*Glycine max*
Strawberry	*Fragaria ananassa*
Sugar beet	*Beta vulgaris*
Sugar cane	*Saccharum* spp.
Tomato	*Solanum lycopersicum* (formerly *Lycopersicum esculentum*)
Walnut (common walnut)	*Juglans regia*
Wheat	*Triticum* spp.