Chapter 15

Pathobiome and microbial communities associated with forest tree root diseases

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Chapter Outline

1. Diverse drivers of microbial change in plants

Soil microbial communities occupy the most biologically diverse habitats in the world. A single gram of soil can support more than several thousand fungal taxa near the root rhizosphere (Buée et al., 2009). As mentioned in other chapters in this book, many factors can influence the microbial communities associated with tree leaves, stems, and roots. Differencesin host species (Prescott and Grayston, 2013), cultivar type within a species, soil type, physiological status of host, and pathogen presence can influence variation in microbial communities (Costa et al., 2007; Aira et al., 2010; Chaparro et al., 2013; Yuan et al., 2015). Ecological balance within the associated microbial community is critical for plant health, especially in the rhizosphere, and disturbances can cause imbalances within the microbial communities. Previous studies have documented that beneficial microbial relationships can enhance seedling vigor, seed germination, plant development, and plant growth that lead to higher plant productivity, whereas attacks by plant pathogens can alter the microbiome structure, functionality, and activity (Trivedi et al., 2012). Beneficial microbial interactions can lead to improved host resistance against pathogenic bacteria and fungi. For example, beneficial microbial taxa can secrete various allelopathic chemicals and toxins that provide the plant with protective barriers that impede plant pathogens. The rhizosphere has been shown to contain diverse and complex biological communities that encompass bacteria, fungi, oomycetes, and many other microorganisms, such as archaea, nematodes, and viruses (Raaijmakers et al., 2009). Other tree organs, including leaves, branches, and stems, are also known to contain a diverse suite of microbial taxa, but overall diversities are typically lower than those found in soils (Baldrian, 2017). Although microbial diversity can vary greatly, pathogens can greatly affect microbial communities. This chapter will briefly review the concept of pathobiome, how microbial communities protect against plant disease, and various changes that can occur within microbial communities in the presence of plant pathogens. Because these research topics are recently developing in forest sciences, examples will be derived from cropping systems as diverse as wheat, apples, and forests. As expected, microbial communities can be vastly different within annual vs. perennial cropping systems; however, the influence of plant pathogens on microbial communities and their ecological roles have been documented primarily in diverse cropping systems.

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2. Pathobiome

Historically, plant disease was thought to result from the interaction of a single host plant and a single pathogen under suitable environmental conditions; however, new sequencing technologies have helped give rise to a new paradigm that plant diseases, in some cases, are the culmination of numerous biological/microbial interactions with the plant host and pathogen that, in concert, reduce host defense mechanisms and/or increase pathogenicity of the pathogen to foster the develop- ment of disease. "Pathobiome" is a term used to describe a consortia of species associated with a host that, when present, reduce host vitality under suitable environmental conditions (Fig. 15.1). Our current capacity to identify species within plant-associated microbial communities has raised awareness on how these microbial communities can affect the fitness oftheir plant host in a myriad of ways, both positively (e.g., increases in survival, growth, and protection from disease) and negatively (e.g., parasitic interactions) (Garbelotto et al., 2019). Factors that drive disease or parasitic interactions include complex relationships among host-associated bacteria, eukaryotes, and viruses under suitable environmental conditions. Also, our considerations of plant disease processes are now also expanding to consider the critical roles of these microbes within these ecological communities. We are currently just beginning to understand how these interactions occur, but they are thought to be very diverse, extremely complex, and variable over time (Bass et al., 2019). Understanding the roles of individual microbes within the pathobiome could result in the development of novel disease mitigation methods. Research efforts are underway to determine how to shift the microbial communities from a "pathobiome" to a more neutral or even beneficial microbiome, which may include methods aimed at synthetically adding new members to the communities with known beneficial properties that increase microbiota-modulated immunity, or adjusting the soil environment to favor naturally occurring, beneficial microbes and/or disfavor detrimental microbes (Vannier et al., 2019). These research efforts offer potential to substantially improve disease mitigation efforts.

FIG. 15.1 The pathobiome is a term to describe a consortia of species associated with a host that, when present, reduce host vitality under suitable environmental conditions. The left side of the tree has a microbial community of nondetrimental microbes "*blue and green circles*." The pathogen *(mustard)* is present but cannot infect. On the right side of the tree, the combination of the microbial community *(red, orange, and yellow* circles*)* and the pathogen *(mustard)* work in concert to cause disease.

3. Soil microbiomes

We have long known that soil microbes play critical roles in forest ecosystems processes. In fact, soil microbes are essential for forest productivity, sustainability, and resilience (Bonan, 2008; Hartmann et al., 2013). Prominent examples of microbial roles in forests include (1) mycorrhizal and bacterial associations that promote plant health and improve tolerance to biotic and abiotic disturbances (Jansson and Hofmockel, 2020; Mendes et al., 2011; Panke-Buisee et al., 2015), (2) decomposition that recycles nutrients (van der Heijden et al., 2006; Yang et al., 2009), and (3) contributions to soil structure (Bahram et al., 2018; Fierer, 2017). However, determining the dynamic composition of microbes in forest soils and understanding the ecological roles of soil microbes represents one of the greatest challenges in forest biology and ecology. Furthermore, microbiota within soils are influenced by countless biotic and abiotic factors, such as temperature, moisture, pH, nutrients, other microbes, plant roots, etc. (Fierer, 2017).

Microbial communities, such as fungi and bacteria, associated with soils and plant roots have been studied for decades. Important microbial taxa associated with plant root systems have been identified, and microbial functions that contribute to plant and soil health are becoming better understood. Key discoveries include microbial functions in nitrogen fixation and ammonia oxidation (De Vries and Bardgett, 2012), and mycorrhizal fungi and/or rhizobia that provide nutrients, protective benefits, and growth stimulation (Dechassa and Schenk, 2004; Dinkelaker et al., 1995). However, with the recent advent of molecular techniques, like metagenomic and metatranscriptomic sequencing, studies examining soil microbial communities with direct sequencing of genomes and transcriptomes can identify genes and their expression in soils along with their potential functions. Studying the metabolomic profile of plant-microbial community interactions has also been established as an important approach for unraveling nonprotein-based metabolites (Chong and Xia, 2017). Mass spectrometry and high performance liquid chromatography (HPLC) are common tools for establishing metabolomic profiles in host-pathogen interactions (Pelsi et al., 2018). Studies using these technologies have markedly increased our knowledge of the chemical and molecular basis for the critical ecological functions that are provided by soil microbes (Chong and Xia, 2017; Jansson and Hofmockel, 2018). Access to the gene composition of microbial communities allows identification and detection of novel biocatalysts or enzymes, networks linking function and phylogeny of uncultured organisms, and evolutionary profiles of soil community function and structure (Jansson and Hofmockel, 2018; Ma et al., 2018).

Studies have documented a strong relationship among soil type, soil physical properties, and geographic location on characteristics and diversity of soil microbial communities, including beneficial and pathogenic fungi and bacteria (Lareen et al., 2016). Several studies have documented greater diversity of microbial communities associated with increasing levels and complexity of organic matter (Lehmann et al., 2020). Further, increasing soil pH, water retention, and nutrients, such as carbon, nitrogen, phosphorus, potassium, and others, have been shown to influence microbial diversity, which has been linked to benefits of disease suppression in some studies (Li et al., 2019; Palansooriya et al., 2019), but variable results have also been observed. Suppressive soils are those in which some members of the soil microbial community help the plant defend against fungal and bacterial pathogens (Baker and Cook, 1974). For example, when examining microbial diversity and richness in disease suppressive soils for a vanilla (*Vanilla planifolia*) cropping system, Xiong et al. (2017) found that bacterial richness and phylogenetic diversity showed positive correlations with soil pH and electrical conductivity, whereas the fungal richness and phylogenetic diversity were negatively correlated with these two soil properties. In another study, comparing microbial diversity in plots with high and low levels of the banana wilt pathogen (*Fusarium oxysporum* f. sp. *cubense*), soil organic matter varied significantly between healthy and diseased plots and was negatively correlated with disease incidence and *Fusarium* abundance (Shen et al., 2019a). Soil organic matter correlated with overall abundance of fungal microbial communities (Shen et al., 2019a). Likewise, in a study examining microbial communities associated with *Armillaria solidipes*, a root disease pathogen, higher fungal richness and phylogenetic diversity were positively correlated with available N, P, and Fe in the soils (Lalande, 2019). The work also showed differences in bacterial communities associated with the nonpathogen (*Armillaria altimontana*) compared to those associated with *A. solidipes* (Fig. 15.2). In general, diverse studies indicate the great complexity of interactions that influence the richness and overall composition of microbes in varying soil types across different geographic areas. Despite these complexities, it is known that soil microbes can help to suppress disease.

4. Plant-pathogen-microbe interactions in disease-suppressive soils

Plant-microbe interactions occur in plant layers, such as the phyllosphere, rhizoplane, and rhizosphere. The plant and plant-associated microbial communities (e.g., bacteria, archaea, viruses, and microbial eukaryotes), which occur above and below ground, are collectively known as the “holobiont”—the genomic reflection of the complex network of symbiotic interactions between the host and associated microbiome (Guerrero et al., 2013; Vandenkoornhuyse et al., 2015). The holobiont

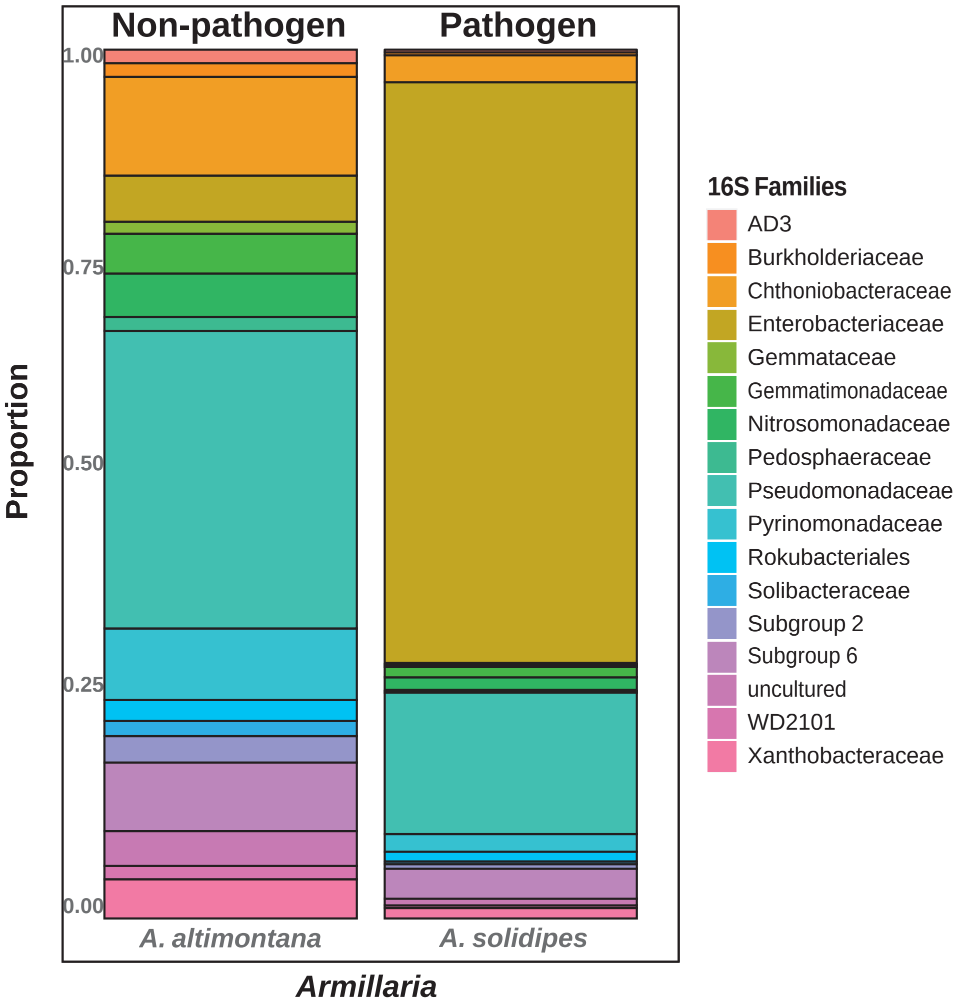

FIG. 15.2 Bacterial communities associated with a nonpathogen (*Armillaria altimontana*) and a forest root pathogen (*Armillaria solidipes*). Soils associated with *Armillaria altimontana* are dominated by beneficial Pseudomonadaceae bacteria commonly found in suppressive soils, whereas soils associated with *Armillaria solidipes* are dominated by pathogenic and saprotrophic Enterobacteriaceae bacterial species.

is formed by selective pressures likely driven by interactions among microbes and the host plant; however, little is known about the contribution of competitive and cooperative microbe-microbe interactions, as these are difficult to interpret even with recent sequencing technologies (Hassani et al., 2018). Contributing to the "rhizosphere effect," plants exude roughly 21% of their photosynthetically fixed carbon at the root-soil interface, which influences the microbial community in the rhizosphere. Typically, a shift from overall diversity of communities to high densities of selected taxa within the community occurs along the gradient from bulk soil to rhizosphere (Mendes et al., 2011). An enrichment of specialized taxa within the community and an overall reduction in the diversity of microbial communities are typically observed in the rhizosphere (Zhang et al., 2017). Plants can provide signals to conspecific, beneficial organisms by producing antifungal effectors and secreting primary and secondary metabolites, such as strigolactones, phenazines, polyketides, and siderophores into the rhizosphere (Carrión et al., 2019), which can cause shifts in the microbial communities that typically vary based on plant species and/or genotypes (Hahl et al., 2020). These plant-driven selective pressures form the basis for microbe-host interactions. Key drivers in the selection of microbes that encompass the holobiont are plant exudates, such as carbohydrates, amino acids, secondary metabolites, and plant-specific flavonoids (Moe, 2013; Weston and Mathesius, 2013). Microbial members of the holobiont can provide plant benefits, such as growth stimulation, stress resistance, nutrient mobilization and transport, and disease suppression via the production of antimicrobial products that can defend against pathogens within the rhizosphere and enhance plant resistance to pathogens (Berg et al., 2014; De Souza et al., 2016; Carrión et al., 2019). Microbes can also elicit host plant responses by symbiotic signaling molecules that can trigger cell wall thickening, programmed cell death, reactive oxygen species (ROS) generation, and production of defense phytohormones and salicylic acid (SA) (Jones and Dangl, 2006; Dodds and Rathjen, 2010; Montiel et al., 2012; De Souza et al., 2016). Additionally, bacteria and fungi produce a multitude of volatile organic compounds (VOCs), like sesquiterpenes (Kramer and Abraham, 2012). VOCs have been shown to disrupt the plants' ability to defend themselves (Bitas et al., 2013). For example, Bitas et al. (2015) showed that VOCs of *Fusarium oxysporum* affected auxin transport and signaling in *Arabidopsis thaliana*. VOCs from plant pathogens such as *Alternaria alternata* and *Pencillium charlesii* can promote starch metabolism, and it is hypothesized that this increases pathogen fitness, but the exact mechanisms are unknown (Ezquer et al., 2010; Bitas et al., 2013). However, structurally diverse VOCs are also known to play roles in defense against other microbes. *Trichoderma asperellum* was shown to significantly reduce disease symptoms of *Arabidopsis thaliana* challenged by *Botrytis cinerea* and *Alternaria brassicicola* (Kottb et al., 2015). Furthermore, Norway spruce (*Picea abies*) hosts a suite of monoterpenes and diterpenes that have antifungal properties and have been shown to decrease infections by *Heterobasidion* sp. (Kusumoto et al., 2014). In general, further studies are needed to better understand the mechanisms of microbiome-induced disease resistance/protection in herbaceous and woody plants.

5. Role of metabolites from bacteria-fungal interactions on plant disease development

Two main types of disease suppression by bacteria and fungi can occur. General suppression, which encompasses the competitive activities of the overall micro- and macroflora, is common in most soils. In contrast, specific suppression, which is typically induced by disease outbreaks on host plants grown on long rotations, results from the enrichment of specific subsets of soil microorganisms (Raaijmakers and Mazzola, 2016). Specific suppression of fungal root pathogens has been attributed to the production of antifungal metabolites by different bacterial taxa, carbon competition, and induced systemic resistance by nonpathogenic fungi. For managing disease risk, it is critical to understand the taxa within suppressive soils that drive competition against pathogens, identify indicators of suppressive soils, and determine taxa that help maintain disease-suppressive soils.

Bacterial taxa within the rhizosphere microbiome have been demonstrated to play critical roles in assimilation of nutrients, resistance to stress, and reduction of disease (Yuan et al., 2015; Zeng et al., 2019). The ability of rhizosphere taxa to reduce plant susceptibility to pathogens has been well documented. Chapelle et al. (2016) documented reduced infection of sugar beet (*Beta vulgaris*) by *Rhizoctonia solani* in suppressive soils, in which microbial communities in *Rhizoctonia solani*-inoculated soils had higher numbers of several bacterial families that have been documented to inhibit fungal growth and protect plant roots from fungal infection. Using mRNA sequencing, these same authors found that HtrA/Sec secre- tion systems, guanosine-3, 5-bispyrophosphate metabolism, and oxidative stress responses were upregulated by the bac- terial families, indicating that bacterial responses that protected sugar beet from infection were triggered by pathogen inoculation in suppressive soils (Chapelle et al., 2016). Another study examining the microbial taxa within *Rhizoctonia*- suppressive soils identified that members of the Pseudomonadaceae protect plants via the production of putative chlori- nated lipopeptides encoded by nonribosomal peptide synthetases (NRPS) genes (Mendes et al., 2011). Burkholderiaceae, Xanthomonadales, and Actinobacteria, which have documented activities against soil-borne pathogenic fungi, were also found within suppressive soils (Mendes et al., 2011). Further, Trivedi et al. (2017) determined that bacteria belonging to the phyla Actinobacteria, Firmicutes, and Acidobacteria were correlated with reduced levels of *Fusarium oxysporum* f. sp. *cucumerinum* within inoculated soils, and these microbial taxa were identified as important indicators of suppressive soils in Australia. Other studies have also implicated Actinobacteria as important in the suppression of Fusarium wilt of strawberry, caused by *Fusarium oxysporum* f. sp. *fragariae* (Cha et al., 2016). Actinobacteria are known to produce numerous antibiotics, enzymes, inhibitors, and plant growth regulators, such as auxins, cytokinins, and gibberellins, that can defend plants against pathogens and contribute to soil health (Sakure and Bhosale, 2019).

Fungi, together with their bacterial symbionts, can also play a strong role in disease suppression, and nearly 80% of land plants are associated with arbuscular mycorrhizal fungi (AMF) (Cameron et al., 2013). Several groups of bacterial symbionts, which are stimulated in the rhizosphere associated with AMF fungi, have also been shown to enhance plant growth and suppress fungal and bacterial pathogens. *Funneliformis*, a genus of AMF, has been found to protect roots against microbial pathogens by priming jasmonate (JA) signaling. *Funneliformis mosseae* has also been shown to enhancegrape vine defenses against nematodes by inducing JA- and SA-inducible defense genes (Li et al., 2006), upregulating SA-independent resistance against *Gaeumannomycetes graminis* in barley (Khaosaad et al., 2007) and tomatoes (Pozo et al., 2002), and enhancing production of benzoxazinoids that defend wheat against challenges by *Rhizoctonia solani* (Song et al., 2011). Other AMF genera have been shown to prime defense-related enzymatic activity and enhance production of phenolic compounds (Abdel-Fattah et al., 2011). In a meta-analysis of 106 scientific studies, Veresoglou and Rillig (2011) demonstrated that AMF on average reduce fungal and nematode damage by 42% and 44%–57%, respectively, thus emphasizing the strong effect of AMF on disease suppression.

Similarly, other fungi, including the ectomycorrhizal (ECM) fungi have been shown to play roles in host defense against soil-borne pathogens. For example, several ECM species, including *Laccaria laccata*, *Hebeloma crustuliniforme*, *Hebeloma sinapizans*, and *Paxillus involutus*, were shown to decrease disease severity caused by root pathogens, *Phytophthora cambivora* and *Phytophthora cinnamomi* on European chestnut (*Castanea sativa*) (Branzanti et al., 1999). Another ECM fungus, *Hebeloma mesophaeum*, was also shown to reduce damage of a rust fungus, *Melampsora laricis-populina*, on the leaves of *Populus* spp. (Pfabel et al., 2012). Kope and Fortin (1989) tested seven ECM as potential inhibitors of 20 phytopathogens. They documented that *Pisolithus tinctorius* and *Tricholoma pessundatum* were antagonistic toward most phytopathogens including root pathogens (e.g., *Armillaria mellea*, *Fusarium oxysporum*, *Rhizoctonia* spp., among others). Although both exhibited inhibitory qualities, *Pisolithus tinctorius* was antagonistic to 85% of the root pathogens, whereas *Tricholoma pessundatum* only suppressed 55% (Kope and Fortin, 1989). A study assessing the differences between natural soils that suppressed *Fusarium oxysporum* and soils that were conducive to the Fusarium wilt disease, Xiong et al. (2017), identified higher levels of *Mortierella*, *Ceratobasidium*, and *Gymnopus* in association to suppressive soil compared to conducive soil. *Trichoderma harzianum*, a common biological fungicide for soil, can be used to inhibit the growth of root pathogens (Grinstein et al., 1979). In a greenhouse and field study, the application of *Trichoderma harzianum*-wheat bran inoculum to previously infested soil successfully protected crops from *Rhizoctonia solani* and *Sclerotium rolfsii* (Grinstein et al., 1979). A field study in British Columbia inoculated *Armillaria ostoyae*-infected stumps with *Hypholoma fasciculare* (an abundant fungus isolated from soil at the site) and results suggested that *Hypholoma fasciculare* can act as direct competitor of the root pathogen, while inhibiting the pathogen spread within soil (Chapman and Xiao, 2000). Two years after the study, one of the sites showed a large reduction in roots infected by *Armillaria ostoyae*, but more time was needed to determine if *Armillaria* could be controlled over the long term with *Hypholoma fasciculare* (Chapman and Xiao, 2000). The use of both bacterial and fungal antagonists, naturally occurring in the soil, may provide an essential biocontrol tool to assist in the overall management of root pathogens.

6. Plant infections by fungal pathogens result in changes in beneficial taxa

Few studies have documented microbial changes that occur after emergence of a plant pathogen, especially in forest ecosystems. Further, studying the interactive effects of plant pathogens on microbial communities is difficult because of the myriad of diverse microbial taxa that are producing a wide array of compounds, and most of the compounds produced by plant pathogens, symbionts, and other associated microbes have not yet been identified and/or characterized. However, evidence shows that some plant pathogens have the ability to shut down beneficial symbionts by deactivating genes involved in antimicrobial production and further weakening symbionts by releasing a suite of secondary metabolites, such as hydrogen cyanide, alkaloids, and bacteriocins (Benizri et al., 2005; Antunes et al., 2008; Holtsmark et al., 2008). This arsenal of compounds can modify the community structure and function, resulting in deleterious impacts for the host plant (De Souza et al., 2016). For example, infections by plant pathogens can cause the upregulation and production of broad-spectrum resistance compounds in the host that can result in the reduction of diverse groups of fungi, bacteria, and viruses residing in the host. This has been observed as pathogen-triggered oxidative bursts in hosts that can result in the production of ROS (De Souza et al., 2016). This activation also results in subsequent induction of endogenous SA. Together, ROS and SA contribute to the production of broad spectrum, multiple-resistance mechanisms. Several studies have found that ROS elevation can result in the decrease of nodulation of rhizobial bacteria in several host plant species (Cárdenas et al., 2008; Lohar et al., 2007; Muñoz et al., 2012). Further, exogenous SA application in alfalfa (*Medicago sativa*) plants resulted in the inhibition of nodule formation (Mabood and Smith, 2007; Hayat et al., 2010), and blocked nodulation by *Rhizobium leguminosarum* in common vetch (*Vicia sativa*) in Norway (Martínez-Abarca et al., 1998).

When examining effects of pathogens on microbial communities, many studies have focused on characterizing bacterial and fungal communities present within rhizospheres of healthy and diseased plants. It is difficult to define trends in changes of microbial community after a pathogen becomes established. In some cases, beneficial taxa within a community are reduced, whereas, in other cases, beneficial taxa remain in association with diseased plants. However, a common result of plant disease is an overall reduction in community diversity and beneficial bacterial/fungal taxa, including Acidobacteria, AMF, and ECM fungi. For example, Huanglongbing (HLB) of citrus, caused by *Candidatus Liberibacter asiaticus* infection, has been shown to reduce bacterial diversity (Trivedi et al., 2012). Further, as described later, changes in microbial communities during infection by pathogenic *Fusarium* species have been documented in several studies.

Similar microbial taxa were identified in association with healthy plants under different cropping systems and across variable geographic locations (Shen et al., 2019a; Xiong et al., 2017). One study focused on continuous cropping systems of banana (*Musa* sp.) where high levels of Fusarium wilt disease caused by *Fusarium oxysporum* f. sp. *cubense* race 4 (FOC 4) have emerged and resulted in reductions of banana yields in China (Shen et al., 2019a). Examinations of microbial communities associated with healthy and diseased bananas found that higher fungal richness was significantly correlated to higher disease incidence; however, potential biocontrol taxa, *Flavobacterium*, *Mortierella*, and Acidobacteria, were negatively correlated with disease incidence (Shen et al., 2019a). In Central America, healthy banana plants were associated with Gammaproteobacteria (Köberl et al., 2017). In China, a reduced level of *Funneliformis*, an AMF in the family Glomeraceae, was also associated with lower yields and higher diseases indexes, which reflects the importance of the AMF in resistance to banana wilt disease. Interestingly, *Mortierella* and Acidobacteria were also found to be important in soils suppressive against Fusarium wilt of vanilla caused by *Fusarium oxysporum* f. sp. *vanilla*. Suppressive soils also had increased levels of general Basidiomycota taxa and taxa within the Zygomycota genus *Mortierella*, which made up 37% of all the DNA sequence reads from suppressive soils (Xiong et al., 2017). Communities associated with Fusarium wilts of banana and vanilla were both associated with higher fungal abundance, richness, and phylogenetic diversity. Similarly, bacterial communities in Fusarium wilt-conducive soils also had higher values for all indices compared to suppressive soils (Xiong et al., 2017). In contrast, banana fields with low incidence of Fusarium wilt of banana in Costa Rica and Nicaragua were characterized with higher microbial diversity in the rhizosphere (Köberl et al., 2017). Further, these fields were also characterized with higher levels of Gammaproteobacteria, in addition to potentially plant-beneficial *Pseudomonas* and *Stenotrophomonas*. Fields with higher levels of disease severity were associated with more *Enterobacteriaceae* taxa (*Erwinia*, *Enterobacter*, and others) (Köberl et al., 2017). Interestingly, soils suppressive for Fusarium wilt of vanilla also had enrichments in some bacterial phyla, including Acidobacteria, Verrucomicrobia, Actinobacteria, and Firmicutes in disease-suppressive soils, while Proteobacteria and Bacteroidetes were more prevalent in the disease-conducive soils (Xiong et al., 2017). Previous studies have documented the importance of Actinobacteria and Firmicutes in the *Rhizoctonia*-suppressive soils (Mendes et al., 2011). Further, Rosenzweig et al. (2012) also found that Acidobacteria were found at higher levels in potato soils that were less conducive to common scab caused by *Streptomyces* spp. (Rosenzweig et al., 2012). Bacterial taxa from the phyla Verrucomicrobia, Actinobacteria, and Firmicutes are known to produce high levels of secondary metabolites and are likely play a role in disease suppression (Kim et al., 2011; Palaniyandi et al., 2013; Shen et al., 2019b).

In other *Fusarium* pathosystems, a different group of bacterial species have also been identified as important in disease suppression. Isolates of *Bacillus* and *Pseudomonas* collected from Lauraceae woody plant species were found to inhibit mycelial growth of *Fusarium solani* and *Fusarium kuroshium*; *Bacillus* sp. collected from the rhizosphere of *Aiouea effusa* produced diffusible compounds that reduced mycelia growth by 62.5% for *F. solani* and 73.6% for *Fusarium kuroshium* (Báez-Vallejo et al., 2020). This study also identified a suite of cloud-forest bacterial taxa, including representatives from *Bacillus*, *Pseudomonas*, *Curtobacterium*, *Microbacterium*, *Arthrobacter*, *Methylobacterium*, *Erwinia*, and *Hafnia*, that produce antifungal compounds that also reduced mycelial growth of *Fusarium* species (Báez-Vallejo et al., 2020).

Other studies have also identified additional taxa that may be important in disease-suppressive soils in other pathosystems. One study examining the microbial taxa within *Rhizoctonia*-suppressive soils identified that members of the Pseudomonadaceae protect plants via the production of putative chlorinated lipopeptides encoded by NRPS genes (Mendes et al., 2011). Burkholderiaceae, Xanthomonadales, and Actinobacteria were also found within suppressive soils and have been documented to have activities against soil-borne pathogenic fungi (Mendes et al., 2011). High levels of *Pseudomonas* were also found in grapevine asymptomatic to esca syndrome, a disease similar to replant diseases of fruit and nut trees (Saccá et al., 2019). The microbial community of barley challenged with *Fusarium graminearum* showed an enrichment of fluorescent pseudomonads and two antifungal/bacterial genes, *phID* and *hcnAB*, that encode proteins that synthesis 2,4 diacetylphloroglucinol and hydrogen cyanide, respectively (Dudenhöffer et al., 2016; Weller et al., 2002). It is hypothesized that plants can actively enrich disease suppression-associated bacterial taxa by exuding chemicals that attract these bacteria via chemotaxis (Dudenhöffer et al., 2016). *Bacillus megaterium* has also been shown to produce hydrogen cyanide and was demonstrated to be present in potato soils that suppress the bacterial pathogen, *Dickeya*, which causes black leg disease of potatoes (Mao et al., 2019).

Rhizosphere soils associated with nursery plantings of diseased and healthy black spruce (*Picea mariana*) were compared via cloned rRNA to determine differences in bacterial and fungal microbial communities, and the microbial communities associated with healthy and diseased seedlings varied considerably (Filion et al., 2004). Interestingly, some fungal operational taxonomic units (OTUs) occurred at high frequency, suggesting that the rhizosphere within nursery soils is dominated by a relatively few fungal species, including *Ossicaulis lignitalis*, *Thelephora* sp., and *Tricholoma myomyces*. A different pattern was observed within the bacterial communities, where more diversity was observed and no dominant OTUs were identified. Rhizosphere communities from healthy plants were dominated by Deltaproteobacteria (Proteobacteria), Eurothiomycetes (Ascomycota), and Pezizomycetes (Ascomycota). In contrast, rhizosphere soils associated with diseased plants were dominated by Nitrospirae (bacteria), Verrucomicrobia (bacteria), Dothideomycetes

(Ascomycota), mitosporic Ascomycota, and Heterobasidiomycetes (Basidiomycota). Overall, reasons for these patterns were difficult to discern due to high diversity within the soils; however, similar to many of the studies reviewed here, bacterial taxa related to *Pseudomonas*, *Bacillus*, and *Paenibacillus*, known biocontrol agents, were only found in association with healthy seedlings (Filion et al., 2004).

Lastly, actinomycetes have been found to be important in suppression of soil-borne pathogens. Across forest soils of scrubby sclerophyll forests, savannah woods, and wetter sclerophyll forests of Australia, reductions of actinomycetes in the presence of *Phytophthora cinnamomi* were correlated with decreasing levels of plant health (Weste and Vithanage, 1978). A survey resulted in the collection of 267 actinomycetes strains, and 15 strains were identified that exhibited antimicrobial properties against *Pythium ultimum* under both laboratory and greenhouse conditions (Crawford et al., 1993). In addition, some actinomycete isolates have displayed antagonistic activities against *Colletotrichum capsici* and *Fusarium oxysporum* (Ashokvardhan et al., 2014), and a *Streptomyces coelicolor* isolate from mangroves in India caused growth reductions of *Aspergillus niger*, *Aspergillus flavus*, *Aspergillus fumigatus*, and *Penicillium* sp. (Gayathri and Muralikrishnan, 2013).

7. Changes in fungal diversity as a response to root pathogens

Some studies also report a higher diversity and/or richness of fungal taxa in the presence of disease. One study examined microbial community differences in Norway spruce asymptomatic and symptomatic to Heterobasidion root disease, caused by an important fungal genus of root pathogens found in Europe and in North America (Kovalchuk et al., 2018). This study compared the microbial communities associated with multiple parts of trees, including the needles, wood, bark, and root systems. In the wood tissues near infection sites, fungal communities and mycelial growth of *Heterobasidion* were significantly different than asymptomatic trees, but differences between asymptomatic and symptomatic trees were not evident in microbial communities of the needles or roots. It is likely that *Heterobasidion* infections progress slowly and microbial changes are localized to the infection area instead of occurring systemically throughout the trees. Additional evidence suggests that *Heterobasidion* infections of Norway spruce in Finland may increase coinfection with other wood-degrading fungi (Kovalchuk et al., 2018). For example, *Inonotus*, a genus of known heartwood decayers, was observed in several of the symptomatic trees. In a study comparing microbial communities associated with *Armillaria solidipes*, a known root pathogen of conifers, and *Armillaria altimontana*, a species that was recently described as a potential antagonist against *Armillaria solidipes* (Warwell et al., 2019), greater fungal diversity was observed in soils associated with the pathogen, *Armillaria solidipes,* which is likely attributable to the increase in saprotrophic fungi (Lalande, 2019). Interestingly, in both studies, little change in the mycorrhizal community was observed, which concurs with findings of Gaitnieks et al. (2016) that infections of *Heterobasidion annosum* and *Heterobasidion parviporum* had limited effects on mycorrhizal colonization or ECM community structure. In addition, Zampieri et al. (2017) examined the effects of infection by *Heterobasidion irregulare*, a nonnative pathogen, and *Heterobasidion annosum*, a native pathogen, on the development of mycorrhizal associations of *Tuber borchii* with Italian stone pine (*Pinus pinea*), and found that infection by either species did not result in a reduction of the number or density of ECM colonizations. Further, another study examining the microbial communities associated with the medicinal perennial herbaceous plant, *Gastrodia elata*, cropping systems found that the presence of *Armillaria* spp., as a mycorrhizal fungus, increased organic matter and decaying wood materials; this symbiosis likely led to increased fungal diversity, but less influence on bacterial diversity was noted (Chen et al., 2019).

8. Changes in bacterial diversity as a response to root pathogens

Root pathogens (fungal or bacterial) can also drive changes in the bacterial microbial community, and unlike the fungal groups, many studies report a decrease in overall bacterial diversity in response to root pathogen. A study examining shifts in bacterial communities of wild rocket (*Diplotaxis tenuifolia*) in suppressive soils and *Fusarium*-infected plants found that overall bacterial diversity decreased in presence of Fusarium disease, with greater number of *Massilia*. After the addition of suppressive soils, a quantitative increase in beneficial bacteria, *Rhizobium, Bacillus, Paenibacillus*, and *Streptomycetes* spp. was observed after only 3 days (Klein et al., 2012). Stump removal as a management tool for stands infested with the forest root pathogen *Armillaria solidipes* (=North American *A. ostoyae*) significantly increased the biodiversity of bacterial communities, suggesting that bacterial diversity is decreased in the presence of *Armillaria* (Modi et al., 2020). When measuring root pathogen effects on microbial communities, most studies focus on root tissues; however, Ren et al. (2019) studied if *Heterobasidion* infections induced bacterial changes in Norway spruce needle, stem, bark, and roots tissues. Interestingly, those authors found that significant changes only occurred in the needle microbial communities. It was hypothesized that bacterial community changes were more apparent in needle tissues because these tissues also had lower species richness, diversity, and evenness compared to the bark, roots, and stem tissues. In that study, the root microbiome was the most diverse and had the largest number of unique taxa (not found in the other tissues), and it was suggested that slow growth of the pathogen may limit change in the bacterial community.

9. Microbiomes linked taxa to the pathobiome

Historically, plant disease was considered to be the result of the interaction between one host and one pathogen. The disease triangle, which highlights the connections among one host, one pathogen, and conducive environmental conditions to cause disease, is a prevailing paradigm in plant pathology that implies that the pathogens work alone when causing disease on a host. However, with the advent of microbiome technologies, more complex relationships among pathogens and their microbial associates have been described as part of the disease process. Amplicon metagenomics (or metabarcoding), for example, allow analyses of complex microbial communities associated with soil, organic debris, rhizosphere, root/stem/foliar endophytes, and phyllosphere in association with forest health and ecological processes (Terhonen et al., 2019). Studies have found that several fungal or bacterial taxa are typically closely connected to the disease status of a host. In some cases, it remains unknown which additional taxa benefit from the diseased status of the host or if these taxa are part of a coinfection process. A complex mix of relationships among additional microbes and disease likely exist for many or most pathosystems. Some studies suggest that the representation of one host and one pathogen in plant pathology should not be a triangle, but rather a square or diamond would better describe the initiation of disease whereby microbial taxa associated with pathogens and their hosts are necessary for disease to occur (Fig. 15.3). Rovenich et al. (2014) suggest that pathogens can utilize effectors of coinhabitants on host tissue for disease expression. Effectors are proteins that plant pathogens secrete to interact with their hosts during invasion (Koeck et al., 2011). Current microbiome sequencing technologies allow the detection of polymicrobial interactions associated with plant diseases. Acute oak decline in Europe, first recognized in the United Kingdom in the 1980s, represents a significant threat to oaks, especially *Quercus robur* and *Quercus petraea*. Isolations from bleeding cankers identified three causal agents: *Brenneria goodwinii*, *Rahnella victoriana*, and an unnamed *Pseudomonas* sp. (Denman et al., 2012, 2014; Brady et al., 2014; Adeolu et al., 2016; Sapp et al., 2016). Bacterial communities associated with the oak decline disease compared to healthy trees also found that *Lonsdalea quercina* spp. *britannica*, *Gibbsiella quercinecans*, and *Rahnella victoriana* were present in high numbers in diseased samples, suggesting their potential roles in disease. All three species were shown through genomics and metatranscriptomic studies to have the genomic capabilities to cause disease and this capability has been demonstrated via Koch's postulates for *Brenneria goodwinii* and *Gibbsiella quercinecans* (Denman et al., 2018). As researchers continue to explore microbial communities associated with plant diseases, more disease complexes will likely be identified, whereby fungal and bacterial species/communities work in concert with each varying component providing specific factors required to cause disease in the hosts.

10. Impact of natural secondary metabolites on pathobiome composition

Secondary metabolites, also called natural products, are organic compounds of low molecular mass that are produced by bacteria (e.g., *Bacillus* spp., *Pseudomonas* spp., and *Streptomyces* spp.), fungi (e.g., *Penicillium* spp., *Aspergillus* spp., *Trichoderma* spp.), and plants of certain taxonomic groups. These metabolites often act as key factors that either

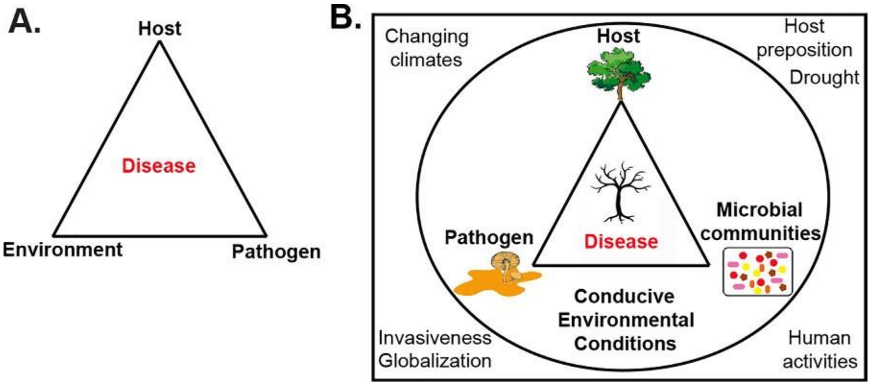

FIG. 15.3 (A) The traditional disease triangle highlighting that a disease can occur when a host and a pathogen on that host are present under conducive environmental conditions. (B) An adapted disease triangle that describes that microbial taxa associated with pathogens and their hosts, in the conducive environment, are necessary for disease initiation. Other factors within the square can also affect a host's susceptibility to disease.

enhance and suppress other organisms (e.g., bacteria, fungi, amoebae, plants, insects, and large animals), which can increase the survival of the organisms that produce them (Demain and Fang, 2000; Peterson et al., 2020). The produc-tion of secondary metabolites is frequently triggered by specific interactions between the organisms under specific circumstances (Peterson et al., 2020). Microorganism- and plant-produced secondary metabolites can influence dis-ease development and suppression, as has been discussed in other parts of this chapter. It has become increasinglyclear that these natural secondary metabolites can alter the structure, composition, and ecological function of thepathobiome, resulting in the increase or suppression of plant disease. A recent review paper emphasized that second-ary metabolites (e.g., coumarins, benzoxazinoids, camalexin, and triterpenes) are responsible for shaping the com- position and function of the plant microbiome. Diverse microbial responses (e.g., microbiome composition, nutrient mobilization, pathogen suppression, and hormonal signaling) can be elicited by variations in secondary metabolite abundance (Jacoby et al., 2021). Research is just beginning to understand the role of secondary metabolites in forest pathosystems, but previous studies indicate that some secondary metabolites could play a crucial role in biocontrolof forest pathogens.

11. Microbial changes in other anatomic regions of trees

Bacterial communities associated with bleeding canker caused by *Pseudomonas syringae* pv. *aesculi* on horse chestnut (*Aesculus hippocastanum*) were significantly different than communities from healthy trees, and overall bacterial diversity was lower in infected trees (Koskella et al., 2017). The authors further suggest that the greater diversity in the bacterial communities of healthy tree hosts may provide protective benefits against bleeding canker. In addition, bacterial communities of olive (*Olea europaea*) change in the presence of olive knot disease caused by *Pseudomonas savastanoi* pv. *savastaonoi* (Pss) (Mina et al., 2020). Comparisons of endophytic and epiphytic bacterial communities showed opposing trends. Endophytic communities changed in response to olive cultivar and the presence of Pss, whereas epiphyte communities remained largely unaffected. The growth behavior of Pss, which occurs in clusters aligned within biofilm-like layers, influenced a change in the endophytic bacterial communities (Mina et al., 2020).

12. Considerations

Soil is one of the most challenging ecosystems to perform metagenomic analyses because of the vast microbial diversity, rhizosphere influences, wide variation in soil properties, and other biotic/abiotic environmental factors that influence microbial diversity and function. This review highlights the extraordinary variation in the number and types of taxa that can even be found in association with the same pathosystems, but from different geographical regions. For this reason, the downstream effects of root pathogens to the overall communities or taxa can vary, depending on the individual ecosystem. Soil physical and chemical properties, such as soil type, pH, and organic matter, must also be considered when comparing results across datasets from different studies and sites. Thus far, few large-scale inferences have been identified from studies on the effects of root disease pathogens on microbial communities, especially within forest ecosystems. However, greater insights will develop as more researchers continue to focus on the complex interactions among microbial communities and root disease pathogens.

Recent developments on co-cultivation of phytopathogens with mixed bacteria-fungi may provide effective strategies for discovering antimicrobial agents with roles in reducing plant disease (Chagas et al., 2013; Vinale et al., 2017). Specific communication between the microorganisms through co-cultures may elicit or induce the expression of previously unexpressed microbial gene clusters associated with producing novel secondary metabolites with potential bioactivity of interest (Bertrand et al., 2014; Netzker et al., 2015). Advanced knowledge of microorganism co-culture, involving the cultivation of multiple microorganisms that are associated with the same host, could be applied to manage plant disease and increase crop and forest productivity (Costa et al., 2019). This biocontrol approach for suppressing pathogens is based on developing disease management methods to favor naturally occurring, biocontrol agents (i.e., microorganisms) and the associated microbes that elicit the expression of genes associated with biological control.

Innovative and integrative approaches are essential for assessing the complex interactions and functions of the microbial communities in forest disease processes in relation to influences of diverse of other environmental factors. Understanding the myriad of interactions among hosts, pathogens, microbial communities, and environments requires unprecedented integration of novel methodologies. Results from such integrated information will help develop novel approaches to manage forest disease and improve forest health by promoting conditions that suppress disease or enhance beneficial microbial and ecological processes.

List of trees and plants

Vanilla (*Vanilla planifolia*)
Banana (*Musa acuminata*)
Western white pine (*Pinus monticola*)
Sugar beet (*Beta vulgaris*)
Barley (*Hordeum vulgare*)
European chestnut (*Castanea sativa*)
Poplar (*Populus* spp.)
Alfalfa (*Medicago sativa*)
Common vetch (*Vicia sativa*)
Citrus
Lauraceae
Aiouea effuse
Potato (*Solanum tuberosum*)
Black spruce (*Picea mariana*)
Norway spruce (*Picea abies*)
Italian stone pine (*Pinus pinea*)
Sessile oak (*Quercus petraea*)
English oak (*Quercus robur*)
Horse chestnut (*Aesculus hippocastanum*)
Olive (*Olea europaea*)

List of microorganisms

Banana wilt pathogen (*Fusarium oxysporum* f. sp. *cubense*) race 4
Fusarium oxysporum f. sp. *vanilla*
Armillaria root disease (*Armillaria solidipes*)
Rhizoctonia solani
Burkholderiaceae
Xanthomonadales
Actinobacteria
Firmicute
Fusarium oxysporum f. sp. *cucumerinum*
Fusarium oxysporum f. sp. *fragariae*
Funneliformis mosseae
Gaeumannomycetes graminis
Laccaria laccata
Hebeloma crustuliniforme
Hebeloma sinapizans
Paxillus involutus
Hebeloma mesophaeum
Melampsora laricis-populina
Pisolithus tinctorius
Tricholoma pessundatum
Trichoderma asperellum
Armillaria mellea
Fusarium oxysporum
Rhizoctonia
Mortierella
Ceratobasidium
Gymnopus
Sclerotium rolfsii
Hypholoma fasciculare
Armillaria ostoyae

Huanglongbing (HLB) of citrus, caused by *Candidatus Liberibacter asiaticus*
Proteobacteria
Bacteroidetes
Streptomyces
Verrucomicrobia
Bacillus
Pseudomonas
Fusarium solani
Fusarium kuroshium
Curtobacterium
Microbacterium
Arthrobacter
Methylobacterium
Erwinia
Hafnia
Bacillus megaterium
Dickeya
Ossicaulis lignitalis
Thelephora sp.
Tricholoma myomyces
Deltaproteobacteria
Eurothiomycetes
Pezizomycetes
Nitrospirae
Paenibacillus
Phytophthora cinnamomi
Pythium ultimum
Colletotrichum capsica
Fusarium oxysporum
Aspergillus niger
Aspergillus flavus
Aspergillus fumigatus
Penicillium sp.
Heterobasidion
Armillaria altimontana
Alternaria alternata
Pencillium charlesii
Heterobasidion annosum
Heterobasidion parviporum
Heterobasidion irregulare
Tuber borchii
Gastrodia elata
Armillaria mellea
Brenneria goodwinii
Rahnella victoriana
Lonsdalea quercina spp. *britannica*
Gibbsiella quercinecans
Pseudomonas savastanoi pv. *savastaonoi*
Pseudomonas syringae pv. *aesculin*
Alternaria brassicicola

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Forest Microbiology

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