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At the roots of chocolate: understanding and optimizing the cacao root-associated microbiome for ecosystem services. A review

Jennifer E. Schmidt¹ · Ashley DuVal¹ · Marney E. Isaac² · Pierre Hohmann³

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Abstract

Crop root-associated microbiomes have been heralded for their potential to improve plant health and productivity. Optimizing beneficial interactions with rhizosphere microorganisms has been proposed to reduce reliance on external inputs, increase pathogen resistance, and alleviate abiotic stresses. Producers of *Theobroma cacao*, the economically important tropical perennial whose pods are used to produce chocolate, are faced with numerous challenges to sustainable production and rising demand. Cacao further provides an interesting case study to complement the extensive plant microbiome research on annual crops in temperate regions. However, current knowledge of the cacao root-associated microbiome is limited. Characterizing the factors that influence the composition and functions of microbial communities associated with cacao roots is a key first step to developing microbiome-targeted interventions for improved agricultural sustainability in cacao agroecosystems. These rhizosphere engineering approaches can be understood within the framework of provisioning, regulating, and supporting ecosystem services. Here we review the potential of cacao root-associated microbiomes to solve current challenges to production by increasing provisioning of ecosystem services. The major points are the following: (1) We describe factors affecting the cacao root-associated microbiome by expanding the traditional model of genotype-by-environment ($G \times E$) interactions to include agricultural management ($G \times E \times M$) and discuss the unique aspects of this model in cacao agroforestry systems. (2) We then highlight how specific breeding targets and management practices can be optimized to enhance the ecosystem services mediated by the cacao root-associated microbiome. Such optimizations of ecosystem services will alleviate the reliance on external inputs and, eventually, contribute to more sustainable cacao production systems.

Keywords Agroforestry · Biocontrol · Breeding; Ecosystem services · $G \times E \times M$ interactions · Plant–microbe interactions · Rhizosphere · Root-associated microbiome · *Theobroma cacao*

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1 Introduction

The tropical tree *Theobroma cacao* is highly valued for its pods, which are used to produce chocolate, cocoa butter, and other commodities of global economic importance (Fig. 1). Though yields have increased slightly over the past 60 years (Kozicka et al. 2018), yield gaps remain significant at up to 82% of yield potential (Aneani and Ofori-Frimpong 2013), and cacao growers remain faced with numerous challenges to sustainable production as well as increasing global demand. Pests and diseases (Bailey and Meinhardt 2016), insufficient soil nutrients (Hartemink 2005; Snoeck and Dubos 2018), pollination limitation (Groeneveld et al. 2010), and the impacts of a changing climate (Lahive et al. 2019) all reduce productivity far below the genetic potential of *T. cacao*. Yield stability is also remarkably low in cacao, with highly variable yields across years and even between adjacent trees (Jones and Maliphant 1958). Yield variability is especially high during juvenile development (Bartley 1970) and not fully explained by soil fertility (Dos Santos et al. 2017). As global demand for cocoa grows at an average of 2.5% per year, these challenges must be addressed without conversion of additional forested or protected area to cacao cultivation (ICCO 2015).

Soil microbial communities, including those in the rhizosphere, are key mediators of ecosystem services (Wall et al. 2012). Interest has therefore grown in “rhizosphere engineering” or leveraging the root-associated microbiome of crop plants to enhance yields and other ecosystem services provided by agriculture (Ryan et al. 2009; Dessaux et al. 2016). Ecosystem services mediated by the root-associated microbiome directly address many of the previously mentioned challenges to cacao production, from increased yields and yield stability (a provisioning service) to disease

suppression (a regulating service) and nutrient cycling (a supporting service) (Fig. 2). As a perennial grown in the tropics, *T. cacao* provides an interesting complement to the extensive plant microbiome literature on annual crops in temperate climates as well as being a crop of global economic importance facing challenges to sustainable production. However, minimal understanding of the cacao root-associated microbiome currently prevents rhizosphere engineering concepts (e.g., via soil management, plant genetics, or bio-inoculation) from being used to enhance delivery of ecosystem services and address production challenges (Hohmann et al. 2020). Culture-dependent methods have been used to identify particular groups of rhizosphere microorganisms, e.g., actinomycetes (Barreto et al. 2008) and arbuscular mycorrhizae (Cuenca and Meneses 1996; Snoeck et al. 2010). Yet amplicon sequencing has been only used to characterize communities associated with other plant and soil regions, such as the phyllosphere (Christian et al. 2017; Santana et al. 2018), endophytic compartments (Rubini et al. 2005; Hanada et al. 2010; Wemheuer et al. 2020), or bulk soil (Mpika et al. 2011; Buyer et al. 2017; Arévalo-Gardini et al. 2020). Numerous studies have also inoculated cacao roots with bacteria and fungi in an attempt to promote plant growth (Supplementary Table 1). Nonetheless, in the absence of comprehensive culture-independent studies, many questions about the cacao root-associated microbiome remain unanswered (Table 1).

Hypotheses about these unanswered questions can be generated by integrating relevant concepts from other crops with a synthesis of the literature on cacao agroecosystems, including microbial communities associated with other parts of the cacao plant (e.g., phyllosphere). These other study systems can provide mechanistic insight in cases where studies have not directly examined the cacao root-associated microbiome. Host genetics, environment, and agricultural management explain some variation in the composition and function of many crop microbiomes, but aspects of these factors unique to cacao agroforestry systems are likely to affect the cacao root-associated microbiome in new ways (Fig. 2, Table 1). In the first half of this literature review, we discuss potential drivers of variation in the cacao root-associated microbiome.

Addressing current challenges to cacao production requires moving beyond the descriptive to the applied: optimizing the cacao root-associated microbiome to enhance the delivery of ecosystem services. Cacao agroforestry systems provide important regulating and supporting ecosystem services (Mortimer et al. 2018) in addition to valuable provisioning services for global consumers of chocolate. Less well understood is how specific breeding activities and management practices shape the potential of the cacao root-associated microbiome to deliver ecosystem



Fig. 1 *Theobroma cacao*. Photograph by Dave Mackill.

Fig. 2 Influences on the cacao root-associated microbiome and its mediation of ecosystem services. Cacao genetics (G), environmental gradients and scales (E), agricultural management (M), and $G \times E \times M$ interactions are likely to contribute to variation in composition and function of the cacao root-associated microbiome. In turn, rhizosphere microorganisms mediate critical provisioning, supporting, and regulating ecosystem services. For further discussion of the processes by which this occurs, refer to Sections 3.1 to 3.3. Figure created with BioRender.

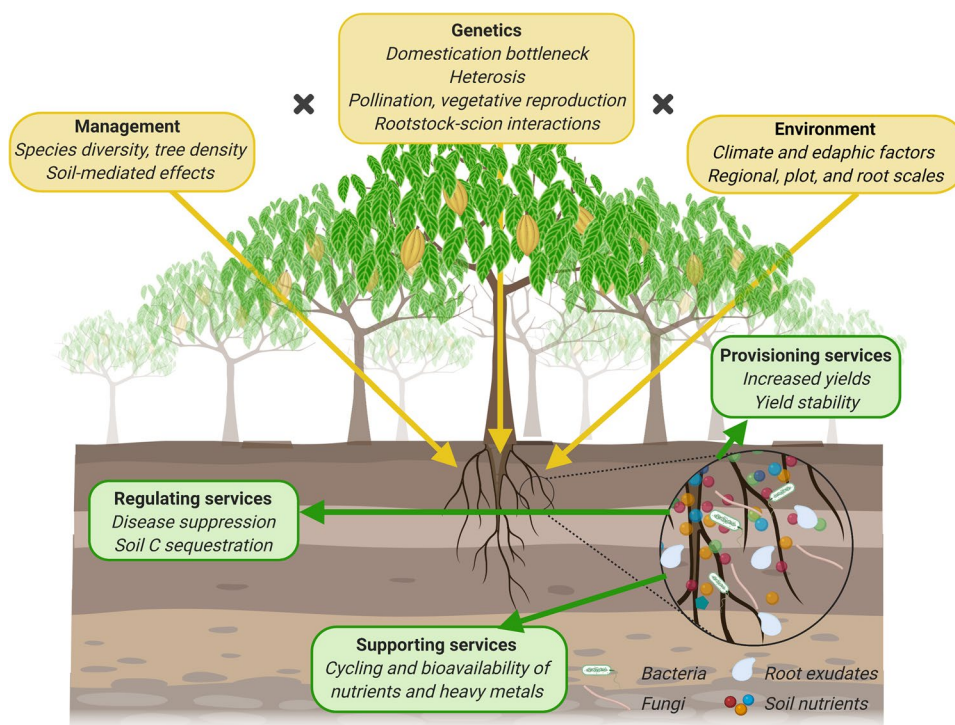
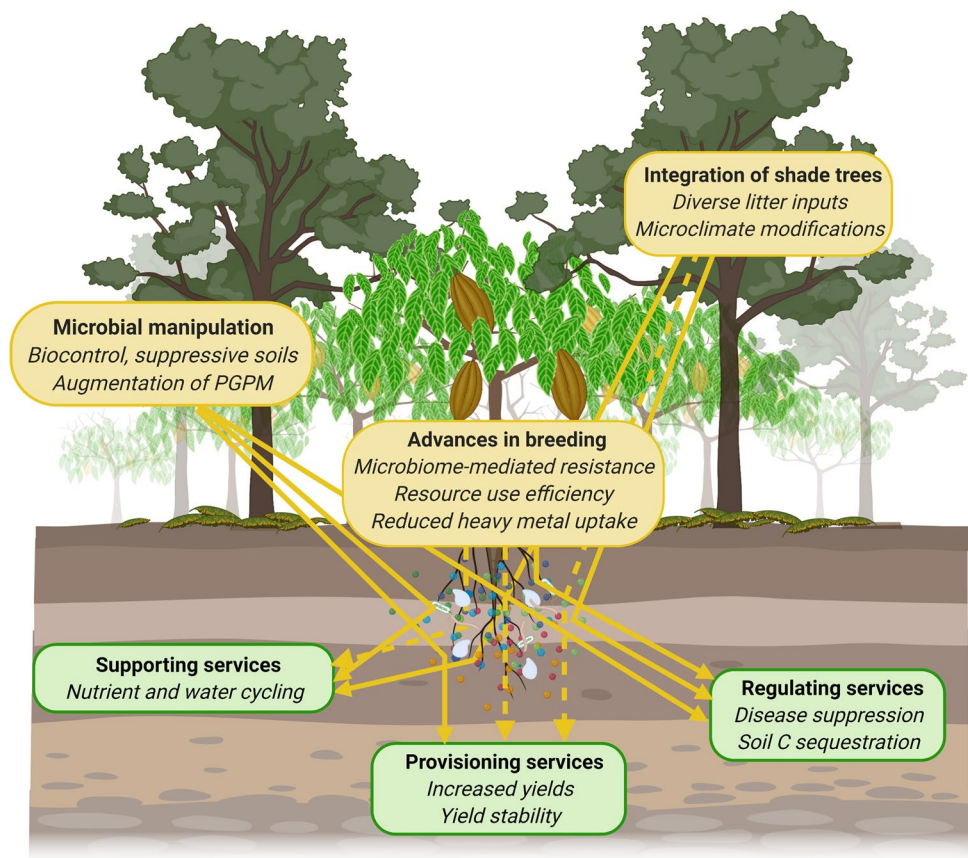


Table 1 Knowledge gaps related to the cacao rhizosphere microbiome.

Core microbiome	<ul style="list-style-type: none"> Which microbial taxa make up the core cacao microbiome (i.e., are present in the cacao rhizosphere across genotypes, environments, and management systems)? Which taxa contribute to variable components affected by host genetics, environment, management, and other factors?
Genetic effects (G)	<ul style="list-style-type: none"> What are the ecological roles and plant-relevant functions of core and variable taxa? How much do cacao genotype, genetic background, and rhizosphere-related traits influence the rhizobiome? How do rootstock and scion identity affect the microbiome, independently and interactively? Do vigorous rootstocks recruit more beneficial microbiota and can rootstock vigor be stacked with microbiome-mediated effects on growth and yield? How have domestication and breeding affected the microbiome of modern commercial <i>T. cacao</i> clones as compared to wild <i>Theobroma</i> spp. and traditional cacao cultivars? To what degree are heritability and heterosis observed on traits associated with the cacao microbiome? What are the mechanisms involved? Can quantitative trait loci for microbiome composition be exploited in breeding (e.g., via marker-assisted selection or genomic prediction)?
Environmental effects (E)	<ul style="list-style-type: none"> How much does the cacao microbiome vary at different scales, i.e., between trees, plots, and growing regions? Which characteristics of the microenvironment have the greatest influence on microbiome composition and function? Is regional microbiome variation linked to sensory properties of chocolate (terroir)?
Management effects (M)	<ul style="list-style-type: none"> How do diversified agroforestry and organic management systems relate to rhizosphere microbiome function?
Regulating services	<ul style="list-style-type: none"> What is the role of cacao rhizosphere microbiome composition in resistance to major cacao pathogens? Can components of the microbiome (e.g., species diversity/composition, key microbial taxa) directly suppress specific pathogens or contribute to indirect mechanisms of pathogen suppression such as induced systemic resistance or disease-suppressive soils? Is disease resistance among rootstocks related to variation in the rhizosphere microbiome?
Supporting services	<ul style="list-style-type: none"> What is the link between known differences among cacao cultivars in nutrient and heavy metal uptake and variation in rhizobiome composition? What are the mechanisms involved, e.g., related to siderophores, rhizosphere, and pH? What exudates might be involved in the recruitment of beneficial taxa?
Provisioning services	<ul style="list-style-type: none"> Can the potential impact of the microbiome on productivity and resilience be specified and quantified?

Fig. 3 Rhizobiome-targeted strategies to enhance ecosystem services. Interventions to optimize the rhizosphere microbiome for enhanced ecosystem services include breeding progress, the integration of shade trees, and microbial manipulation. Solid arrows represent direct effects and dashed arrows represent indirect effects. C, carbon; PGPM, plant growth-promoting microorganisms. Figure created with BioRender.



services (Fig. 3). In the second half of this literature review, we present strategies that could be used to enhance microbiome-mediated ecosystem services in cacao agroforestry systems and discuss the processes responsible.

2 Drivers of variation in the cacao root-associated microbiome

2.1 Host genetics (G)

The genetic identity of the host plant has a significant influence on the composition of the root-associated microbiome at both species and genotype levels (Bouffaud et al. 2014). The strong domestication bottleneck (reduction in genetic diversity due to founder effects during dispersal or selection) associated with certain common cultivars, the potential for heterosis in modern hybrids, the combination of sexual and vegetative reproduction, and rootstock-scion interactions may all impact the *T. cacao* root-associated microbiome (Table 1).

Domestication greatly reduced host genetic diversity among the first Criollo, Amelonado, Nacional, and Trinitario cultivars grown by Central and South American civilizations in comparison to the diversity present in the Upper

Amazon, likely the center of origin of cacao (Motamayor et al., 2002; Motamayor et al., 2008). Sequence data from 200 wild and domesticated cacao accessions has provided additional evidence that strong bottleneck events have given rise to cultivars with levels of homozygosity considered high for an outcrossing tree species (Cornejo et al. 2018). Two examples include the first two sequenced cultivars, Matina 1–6 and Criollo 22, which are both highly homozygous and complementary, sharing less than 30% of their alleles (Argout et al. 2011; Motamayor et al. 2013). Nonetheless, it remains to be seen whether these broad differences in cacao genetic backgrounds and particularly fixation of different alleles through bottlenecks and domestication have led to reduced microbiome diversity or changes in plant-relevant functions of the root-associated microbiome. Some of these outcomes have been observed in the modern cultivars of other species, for instance, in the increased relative abundance of Proteobacteria and Actinobacteria and decreased relative abundance of Bacteroidetes in many crops (Pérez-Jaramillo et al., 2018), and the decreased β -diversity of the modern maize rhizosphere microbiome as compared to its wild ancestor (Schmidt et al. 2020).

Modern breeding has had a relatively short history in cacao, with the first selections and crosses made in Trinidad in the 1930s (Bartley 1994). Nonetheless, the development

of germplasm collections from farmers' selections and wild collections and the development of hybrids from divergent genetic backgrounds may have impacted the root-associated microbiome. Molecular markers have allowed cacao germplasm to be classified into ten primary genetic groups with subgroups: Amelonado, Contamana, Criollo, Cururay, Guiana, Iquitos, Marañón, Nanay, Nacional, and Purús (Motamayor et al., 2008; Zhang & Motilal, 2016). Even though current breeding programs utilize a very small percentage of the extant genetic diversity of the species, progress has still been made in the generation of high-yielding, disease-resistant cultivars such as CCN-51 in Ecuador and R4 in Costa Rica (Phillips-Mora et al. 2009; Boza et al. 2014). Hybrids generated from genetically distant parents can show heterosis for cacao yield components including wet bean weight per plant and wet bean weight per pod (Dias et al. 2003). Though studies on heterosis in perennial microbiomes are lacking due to the long timeframes required for perennial breeding programs, heterosis may extend to features of the cacao microbiome, as is the case for the maize rhizosphere and phyllosphere microbiomes (Wagner et al. 2020). In maize, rhizosphere bacterial and fungal communities differ between inbreds and their F1 hybrids. Furthermore, heterotic effects on alpha and beta diversity were observed, and specific features of the rhizosphere and leaf microbiomes showed midparent or better-parent heterosis, with greater heritability in the rhizosphere than phyllosphere.

The two major strategies employed in cacao breeding, open/controlled pollination and vegetative propagation (Laliberté and End 2015), likely impact the root-associated microbiome in very different ways. First, crosses made through pollination can generate novel genotypes that may be hard to predict, as cacao is highly heterogeneous and often does not breed true to type (Boza et al. 2013). Some degree of heritability has been found for the microbiome of a short-lived wild perennial (Wagner et al. 2016). However, against the complex background of cacao genetics, incompatibility mechanisms, and field mortality that contribute to imbalanced trial design, along with high levels of GxE, the signal of heritable microbial taxa may be difficult to discern.

Even when vegetative propagation is used, selected scions are invariably grafted onto heterozygous rootstocks from uncontrolled pollinations. Vegetative propagation of desirable clones onto rootstocks, which alters whole-plant physiology, are likely to contribute another level of complexity to the root-associated microbiome due to potential effects of rootstock-scion interactions. Grafting reorganizes xylem tissue, lowering hydraulic conductivity of graft tissue relative to the scion, and altering movement of water, ionic solutes, and growth hormones (Atkinson et al. 2001; Martinez-Ballesta et al. 2010). Rootstocks can affect scion gene expression and vigor, increase fruit quality, improve yields and resource use efficiency, contribute new genetic

variation through epigenetic effects, and confer resistance to pathogens and abiotic stresses such as drought, salinity, and heavy metal contamination (Cookson and Ollat 2013; Gregory et al. 2013; Albacete et al. 2015; Warschefsky et al. 2016). Although studies of grafted cacao have not evaluated the microbiome, studies in grafted apple, grapevine, and tomato show that rootstock genotype has a small but significant effect on the composition of rhizosphere and/or endophytic microbial communities (Marasco et al. 2018; Liu et al. 2018; Poudel et al. 2019). Changes in root exudates may be responsible, as seedlings grafted to rootstocks differ in the quantity and quality of rhizodeposits in comparison to autografted seedlings (Song et al. 2016; Leisso et al. 2017, 2018). Given that rootstock affects yield-related traits in cacao (Yin 2004, Romero Navarro et al. 2017), studying the impacts of vegetative propagation on the cacao root-associated microbiome could help illuminate whether vigorous rootstocks are aided by a greater number of growth-promoting microorganisms (Table 1).

2.2 Environment (E)

Heterogeneous environmental conditions can shape distinctive structural and functional characteristics of highly responsive plant root systems and root-associated microbial communities. Such environmental effects act along a range of scales: the broad climato-edaphic conditions, the management strategies at the plot scale, and the responsive root scale (Fig. 2). This plant environment scale is then disaggregated into further levels of analysis: the distribution of the whole root system in the soil profile, the growth and morphology of lateral roots, and the sites of exchange on absorptive roots. Each of these scales shapes various components of root-associated microbial communities. Plant identity and substrate hotspots explain microbial community composition at the local scale, while climate, topography, and soil pH explain variability in microbial communities at the regional scale (de Vries et al. 2012), with soil type being more influential on the microbiome than host phylogeny (Yeoh et al. 2017).

Tropical soils pose unique agricultural management challenges, including low organic matter, nutrient imbalances, and acidity. These factors shape the bulk soil microbial community from which the rhizosphere microbiome is recruited, but the degree to which geographic variation affects rhizosphere bacteria and fungi that are also influenced by cacao roots and root-environment interactions has rarely been studied. Notably, the relative abundance of different genera of mycorrhizal fungi differs between cacao grown in tropical dry and moist forests (Guillermo Ramírez et al. 2016), indicating that root-associated fungal communities are sensitive to regional differences in precipitation. Host-mediated indirect effects on the cacao microbiome are also

likely; environmental factors account for as much as 70% of annual variation in cacao yields (De Almeida and Valle 2007), and the proportion of variation attributable to environment as opposed to genetics differs among yield components (Doaré et al. 2020). Significant variation in cacao phenotypes and flavor precursor compounds occurs among climatic regions and soil types (Clapperton et al. 1994; Afoakwa et al. 2008; Aprotosoie et al. 2016). Terroir has similarly been linked to the soil microbiome in wine grapes (Bokulich et al. 2016), and a recent review highlighted geographic differences in microbial communities responsible for cacao fermentation (Viesser et al. 2021), suggesting potential relationships between geographic variation in the cacao phytobiome, fermentation microbiome, and chocolate flavor profiles (Table 1).

While these bidirectional interactions (plant to environment and environment to plant) clearly influence broad microbial communities, it is the fine scale zone—site of direct plant-soil interaction in the rhizosphere—that is continuously influenced by plant roots through the rhizodeposition of exudates, mucilage, and sloughed cells (Bais et al. 2006; Uren 2007; Moe 2013). Results predominantly show that higher rhizodeposition leads to higher microbial diversity (Paterson et al. 2007) and strong effects on pore geometry (Feeney et al. 2006). Simultaneously, changes in the root-associated microbial community can influence the plant both directly, by producing regulatory compounds, and indirectly, via decomposition and the rate of accumulation of organic material (Hinsinger et al. 2009). We also know that important shifts in root trait expression have consequences for root exudates and rhizosphere chemistry, which can in turn impact root-associated microbial communities. For instance, Fulthorpe et al. (2020) showed that *Coffea arabica* has an identifiable core microbiome and that fungal and bacterial communities varied with key root traits and environmental factors along a climatic gradient.

2.3 Management (M)

Evidence supports a suite of ecosystem functions and services derived from shade tree pairings, including yield stability, climate regulation, disease mitigation, and localized soil fertility (Vaast et al. 2016; Somarriba and Lopez-Sampson 2018; Andres et al. 2018; Isaac and Borden 2019; Niether et al. 2020). Shade trees provide diverse litter inputs that increase soil organic matter, leading to improved C sequestration (regulating service) and nutrient cycling (supporting service) as discussed in the context of management impacts on the cacao root-associated microbiome. Shaded cacao systems range from monocultures to diverse shade-tree systems, dominated by N_2 fixing species, timber species, and fruit trees (Sauvadet et al. 2020a). In particular, leguminous tree roots and nodules contribute

substantive nitrogen sources to soils in agroforestry systems, from direct pathways via N-rich root exudates or common mycorrhizal networks or from indirect pathways via litter, root and nodule decomposition, and mineralization processes (Isaac and Borden 2019). However, given the heterogeneous conditions in which shade tree selection is made, there is the inconsistent evidence on cacao agroforestry success, suggesting a potential tradeoff between provisioning and regulating services (Ruf 2011; Blaser et al. 2017; Abdulai et al. 2018). Yield of cacao may be lower by around 25% in agroforestry systems, but total system yields are tenfold higher (Niether et al. 2020), demonstrating an indirect positive effect on provisioning services (Fig. 3). While an increase in pests and diseases is often attributed to agroforestry systems, negative effects on this regulating service can be avoided with appropriate phytosanitary measures such as pruning and diseased pod removal (Armengot et al. 2020).

Increased genetic and phenotypic diversity of roots in shade tree systems is likely to impact the microbiome, as microbial taxa vary across root phenotypic trait gradients (Saleem et al. 2018) and differ among tree species (Si et al. 2018). Research into the effects of shade trees on the cacao rhizosphere has largely focused on shifts in root architecture (e.g., depth, distribution) or allocation to root mass (e.g., root to shoot ratio) in different species combinations (Moser et al. 2010; Schwendenmann et al. 2010; Isaac et al. 2014; Abou Rajab et al. 2016, 2018; Borden et al. 2019). Emerging research also shows the effects at the cacao root scale (e.g., root morphology (Abou Rajab et al. 2018)) and coordinated root trait response (Borden and Isaac 2019). Borden et al. (2019) showed that proportionally more biomass was allocated to roots for cacao grown in mixture with shade trees in comparison to cacao in monoculture, with strong associations of greater root length and biomass densities to specific cations (higher NH_4^+ and Ca^{2+}). Furthermore, findings show a tendency for cacao roots to express acquisitive morphological root traits and higher root turnover rates in agroforestry systems. Abou Rajab et al. (2018) observed this trend in cacao grown in multispecies mixture, although an opposite trend was observed for cacao in mixture with only *Gliricidia sepium*. Based on research on other tree crop species (coffee; Fulthorpe et al. 2020), these key variances in root morphological and chemical response to environmental conditions and shade tree management impact the microbiome via root and rhizosphere processes. Presumably, these root-scale adaptations in agroforestry systems have strong effects on the root-associated microbiome, but this remains nearly completely unstudied. Wartenberg et al. (2017) found no significant relationship between tree diversity in cacao agroforestry and measures of microbial abundance. In contrast, Buyer et al. (2017) report that various agroforestry systems (with varying degrees of plant diversity) affected biological

changes in the soil; higher plant diversity was linked with higher gram-negative to gram-positive ratios. However, both of these studies were restricted to bulk soil. Further work needs to assess these measures in the rhizosphere of cacao under shade trees in order to determine the impacts of agroforestry on the cacao root-associated (Table 1).

The impacts of agricultural management on the cacao root-associated microbiome may be most clear at regional and plot scales. In a study of different cacao agroforestry systems within five regions of Cameroon, Wemheuer et al. (2020) found that management had stronger impacts than environmental variation on bacterial and fungal endophytes of *T. cacao*. In other perennial microbiomes, direct impacts of management depend on the study system and the specific practice of interest: Collier et al. (2019) report that both management practices and geography shape the microbiome of vineyards, while Köberl et al. (2015) showed that neither biogeography nor various plot-scale management conditions (agroforestry) impacted the core microbiome of bananas.

Management practices that alter soil properties such as organic matter, pH, and moisture can affect the cacao root-associated indirectly (Fig. 2). Soil organic matter from aboveground litter and belowground root inputs provides nutrients and energy to microbial communities, and amendment practices such as conventional fertilization or organic inputs can control microbial populations in the rhizosphere of tree crops (Munroe et al. 2015). Organically managed cacao agroforestry systems have 20% more soil organic carbon (Asigbaase et al. 2020) and four times more root biomass (Niether et al. 2019), which may account for the increased bacterial and fungal diversity in these systems (Suwastika et al. 2019). Similar effects on microbial diversity and abundance due to organic matter could be expected from the litter and pruning residues in diversified agroforestry systems relative to monocultures, which can add up to ten times as much nitrogen to surface soil as fertilizer inputs (Schneidewind et al. 2019). Conversely, continuous cropping that depletes soil organic matter and nutrients may have opposing effects on the diversity of the root-associated microbiome. In a study in Ghana following 17 years of continuous cropping of Amelonado, there was a loss of nearly 55 t of humus ha⁻¹ and a depletion of more than 66% of the exchangeable bases in the soil profile as compared with an adjacent fallow (Ahenkorah et al. 1974). Nutrient input requirements increase considerably as shade levels decrease, and classic studies show that yields start to decline in conditions with over 50% lighting without the addition of fertilizers (Murray 1954; Evans and Murray 1955). Liming is commonly recommended in cacao production regions with acid soils such as Malaysia and Brazil to increase nutrient availability (van Vliet and Giller 2017). This practice likely impacts composition and functions of the cacao

root-associated microbiome, as soil pH is a key driver of microbiome composition (Fierer and Jackson 2006) and influences microbial carbon cycling (Malik et al. 2018). Plot scale management practices affecting water availability can also shape a crop microbiome in tree-based systems: Furze et al. (2017) showed that core AMF communities associated with soybean experienced significant shifts with water restrictions but only in tree-based agroecosystems.

3 Enhancing ecosystem services with the cacao root-associated microbiome

There are various opportunities to enhance ecosystem services in cacao agroforestry systems via interventions at the plant-soil interface (Fig. 3). Strategies such as breeding for specific microbe-related traits and functions, integration of shade trees, and manipulation of soil microbial communities vary in the directness and relative magnitude of their impacts on each category of ecosystem services. One direct route to enhancing disease suppression (regulating) or plant growth promotion (provisioning) would be to identify and augment the taxa responsible for those functions. While breeding for microbiome-mediated disease resistance could likewise directly impact disease suppression (regulating), breeding for resource use efficiency would affect nutrient cycling (supporting) and yield (provisioning) indirectly. Introducing shade trees and their diverse leaf litter, which serves as the substrate for numerous microbial metabolic processes, would have the strongest direct impacts on soil C sequestration (regulating) and nutrient cycling (supporting).

3.1 Provisioning services

3.1.1 Sustainable productivity

The growth-promoting potential of rhizosphere bacteria and fungi has long been of interest in many crops, and selected microorganisms are available as biofertilizers. These plant growth-promoting microorganisms (PGPM) are thought to act through both direct mechanisms, e.g., increasing plant access to nutrients by solubilizing phosphate and potassium or stimulating root growth, and indirect mechanisms such as pathogen suppression or enhanced abiotic stress resistance (Lugtenberg and Kamilova 2009). Increasing the abundance of PGPM would have a positive direct effect on yield (provisioning services, Fig. 3). Studies testing the effects of PGPM inoculation on cacao productivity are rare, however, and have frequently measured biomass at seedling stages rather than pod production or other yield components (Supplementary Table 1). Furthermore, cacao yields are characterized by high levels of tree-to-tree variability. Even within

plots of clonal trees, high levels of unaccounted-for variation have long been observed (Jones and Malipant 1958; Murray and Cope 1959). Some studies have demonstrated that yield parameters correlate strongly with certain key nutrient concentrations in different soil horizons (Vanderlei et al. 2003) and with leaf functional traits (Sauvadet et al. 2021). The potential role of the root-associated microbiome in improving yields and stabilizing productivity through contributions to nutrient cycling and water availability deserves further study (Table 1), especially considering that the longer lifespan of perennials and consistent presence of roots throughout the year are thought to make rhizosphere interactions more durable in tree crops than in annual crops (Mercado-Blanco et al. 2018).

3.2 Regulating services

Recent ecosystem services research in biodiverse and well-designed agroforestry systems suggests ecosystem services extend beyond production alone. Key microbiome-mediated processes associated with regulating and supporting services are evident, yet understudied in cacao agroecosystems. Major regulating services that could be enhanced by the rhizosphere microbiome include disease suppression and carbon sequestration.

3.2.1 Microbiome-mediated disease resistance

Biological control and disease-suppressive soils Globally, pests and diseases constitute a major threat to cacao production, accounting for at least 20–30% of lost production annually (Ploetz 2006). Many of the most devastating cacao pathogens primarily affect pods, leaves, or other aboveground tissues, while one major pathogen (*Phytophthora* spp.) and numerous minor pathogens have soil-borne stages (Supplementary Table 2); the root-associated microbiome has the potential to act against both aboveground and belowground pathogens. Manipulation of the cacao root-associated microbiome to promote disease-suppressive taxa (e.g., biological control and suppressive soils) can complement breeding for rootstock resistance and microbiome-mediated resistance, a strategy with strong direct impacts on this regulating service (Fig. 3). For example, rhizosphere populations of mycoparasites are independent of cacao genotype and could thus be manipulated separately (Ten Hoopen and Krauss 2016).

Biological control, where specific bacterial or fungal taxa are applied as a preventative measure or augmented from the existing microbial community, is the primary way in which the microbiome has been managed to control cacao pathogens to date (e.g., Crozier et al., 2010; Loguerio et al., 2009; Melnick et al., 2011; Suryanto et al., 2014). Microbial biocontrol agents (BCA) deliver protection against the target

pathogen via direct mechanisms of action, such as mycoparasitism and antibiosis, or indirect mechanisms including competition for rhizosphere resources and induced systemic resistance (Compant et al. 2005; Shores et al. 2010). Biological control studies have been conducted on many major cacao pathogens, particularly *Phytophthora* spp., *Moniliophthora perniciosa*, and *M. roreri* (Supplementary Table 2), and while these studies have mostly been conducted aboveground, the direct and indirect mechanisms involved would likely be effective belowground as well.

Induced systemic resistance by rhizosphere bacteria and fungi, an indirect mechanism of biological control, has been reported in other tree species (Jetiyanon and Kloepper 2002; Eyles et al. 2010; Shores et al. 2010). Despite the challenges of implementing biological control in woody perennials (Hohmann et al. 2012; Cazorla and Mercado-Blanco 2016), high rates of promising BCA in the phyllosphere (Hanada et al. 2010) and moderate success in cacao trials to date (e.g., Melnick et al. 2008) suggest that BCA could be a promising component of integrated pest management in cacao. To reduce discrepancies in results between controlled and field conditions (e.g., Krauss & Soberanis, 2001), future studies should screen potential BCA under field-relevant conditions, as sterile settings may favor colonization traits over competitive traits that enhance soil persistence (Ten Hoopen and Krauss 2016). Furthermore, such studies should clarify the underlying mechanisms and context dependency of pathogen-BCA relationships (Hohmann et al. 2020) to guide decisions about managing the rhizosphere microbial community (Allen Herre et al., 2007). If specific beneficial microorganisms inhibit the pathogen directly, the emphasis should be on identifying those microorganisms and clarifying the biochemical nature of the inhibition. In contrast, if pathogen suppression is due to indirect mechanisms, increasing total microbial abundance is likely more important than introducing individual taxa.

Certain aspects of the phyllosphere may favor direct mechanisms of BCA action in comparison to the rhizosphere. First, microbial communities are relatively sparse in the harsh environment of the phyllosphere (10^6 – 10^7 organisms cm^{-2} leaf, (Lindow and Brandl 2003)) in comparison to the comparatively well-populated rhizosphere (10^8 – 10^9 organisms g^{-1} soil, (Berendsen et al. 2012)). Microbial BCA applied to leaves and pods may thus outnumber other microorganisms, increasing the frequency of BCA-pathogen interactions that lead to pathogen inhibition. In the rhizosphere, denser microbial communities may enable pathogen persistence through a greater frequency of neutral interactions or by outcompeting introduced BCA. Resource limitation in the phyllosphere also appears to be important for successful biocontrol, as the effectiveness of inoculation against foliar pathogens such as *Pseudomonas syringae* is reduced in fertilized plants (Berg and Koskella 2018). Most foliar

endophytic fungi in cacao also function by outcompeting pathogens for resources, with 27–65% of endophytic isolates showing antagonistic activity such as resource competition but only 0–21% showing direct antibiosis against the major cacao pathogens *M. perniciosa*, *M. royeri*, or *P. palmivora* (Mejía et al. 2008). In the rhizosphere, exudation of organic compounds by roots and fertilization of agricultural fields create a comparatively resource-rich environment where bio-control strategies should not rely on nutrient limitation to succeed. Alternative approaches to biocontrol should thus be investigated for soil-borne pathogens of cacao, which have been neglected in comparison to aboveground studies thus far (Supplementary Table 3).

Even with the recent shift from externally applied bio-control agents to endophytes that may provide longer-lasting benefits, Ten Hoopen and Krauss (2016) argue that biological control will only be one component of disease management strategies, as substantial improvements in formulation and application techniques are needed for it to become economically relevant. The native cacao endophyte *Colletotrichum tropicale* induces systemic changes in gene expression related to pathogen defense (Mejía et al. 2014), and the protection it confers against *Phytophthora palmivora* can be transferred to endophyte-free seedlings via leaf litter from colonized trees (Christian et al. 2017). Increasing the abundance and persistence in soil of *C. tropicale* or other rhizosphere microorganisms capable of inducing systemic resistance could therefore be important rhizosphere engineering strategies.

The establishment of disease-suppressive soils provides an indirect mechanism by which the cacao root-associated microbiome could prevent disease. Observed in perennial crops including apple, suppressive soils are a phenomenon by which a cropping system exposed to a given soil-borne pathogen shifts over time such that the soil microbial community eventually confers disease resistance to the host plant. Weller et al. (2002) distinguish between general suppressiveness, which is regulated by total microbial biomass and is non-transferrable, and specific suppressiveness, which is provided by a subset of microbial taxa and is transferrable between soils. In contrast to biological control, suppressiveness is frequently related to complex shifts in community composition involving many taxa rather than a single culturable organism (Kinkel et al. 2011). While no suppressive soils have been reported in cacao to our knowledge, bioinformatics approaches and multivariate analyses should be implemented for the cacao root-associated microbiome to identify and enhance potential mechanisms of resistance rooted in microbial ecology.

Breeding for disease resistance Despite observations of disease resistance in numerous cacao cultivars, progress in stacking traits and breeding for resistant rootstock has been

encumbered by poor overlap in genotypes between contrasting sites, different criteria for phenotypic screening, seasonal fluctuations in the levels of pathogen inoculum present, limited knowledge of potentially beneficial endophytes, and the confounding factors introduced by a poor understanding and characterization of open-pollinated rootstock. Pre-breeding and parental selections for resistant lines can be complicated by inconsistencies in reported phenotypes and heritabilities around disease traits, which are evident in conflicting records in databases compiled from multi-locational breeding trials such as the International Cacao Germplasm Database (www.icgd.rdg.ac.uk). This variability has been attributed to the prevalence of offtypes in collections (DuVal et al. 2017) and different approaches used in screening but also highlights an opportunity to explore the potential role of the root-associated microbiome on expression of disease traits for resistance breeding. Careful, controlled studies to better isolate and understand the relative contributions of environment, rootstock genetic effects, and plant–microbe interactions will be key in understanding the expression of complex resistance and tolerance traits.

While the role of plant-associated microbes for crop disease resistance is well recognized (e.g., Mendes et al. 2011; Berendsen et al. 2012; Pieterse et al. 2016), host regulatory mechanisms that shape a beneficial or detrimental plant microbiome remain largely underutilized. There is increasing evidence for an exploitable genetic base for plant responsiveness to native soil microbiomes that plays a significant part in driving root-associated microbial community composition and activity (Aira et al. 2010; Bulgarelli et al. 2015; Walters et al. 2018; Wille et al. 2019). More specifically, genotypic differences in the regulation of beneficial plant–microbe interactions of various crops were shown for microbe-mediated resistance by individual strains (Sefloo et al. 2019) or entire communities (Elhady et al. 2018), responsiveness to soil microbial feedbacks (Hu et al. 2018), and microbe-induced resistance priming (Shrestha et al. 2019). There are opportunities for cacao resistance breeding programs to exploit this genotypic variation for enhanced ecosystem services (Fig. 3). Thus, new breeding strategies are called for in order to unravel hidden parts of complex holobiont defense mechanisms.

Recent studies have identified plant quantitative trait loci (QTLs) that explain microbiome structure as a first step towards marker-assisted selection (Lebeis 2015; Stringlis et al. 2018; Hu et al. 2018; Bulgarelli 2019; Wehner et al. 2019; Zhang et al. 2019; Chen et al. 2020). Recent advances in genotyping technologies will allow the discovery of genomic loci and candidate genes involved in plant-microbiome interactions beyond model species. For instance, Bulgarelli (2019) reported a single QTL responsible for the recruitment of specific members of the microbial community, and

Wehner et al. (2019) identified a QTL for microbe-induced leaf rust resistance. Combining plant genomic resources with metagenomic data of the associated microbiome can lead to the development of resistance markers in breeding programs. However, plant domestication and breeding under optimal supply of inputs such as synthetic fertilizers might have unintentionally selected against functional traits of the plant-associated microbial community (Morgan et al. 2005; Bennett et al. 2013; Bulgarelli et al. 2015; Schmidt et al. 2016; Pérez-Jaramillo et al. 2016; Hohmann and Messmer 2017). That is why it is crucial to integrate the microbial community of the target environment in early selection processes. The efficiency of microbiome-supported selection depends on the heritability of the trait. For instance, Wagner et al. (2016) showed significant $G \times E$ interaction effects of wild perennial mustard (*Boechera stricta*) on microbiome community composition. The integration of the microbiome in the basic phenotype model $Y \sim G \times E$ can occur by disentangling E to include plant \times microbe and plant \times microbe \times environment interactions (Wille et al. 2019). Oyserman et al. (2021) proposed to expand the classical model by adding the microbiome (MB) as an explanatory factor, $Y \sim G \times E \times MB$, thus, explaining plant yield as a function of the genotype, environment, and microbiome interactions. For cacao, the model can be extended to account for possible interactions of rootstock (G_R) and scion genotypes (G_S) as well as management system (M): $Y \sim G_R \times G_S \times E \times MB \times M$.

Currently available cacao varieties have not specifically been selected to engage with a beneficial root-associated microbiome, partly as a result of common farming practices that either directly suppress microbes (e.g., via fungicide applications) or hamper their engagement (e.g., due to the application of easily available nutrients). Plant-driven shifts of the microbial community are linked to environmental factors such as climatic conditions, soil composition, or crop management (along with plant physiological and phenological effects) and can be utilized in breeding for local adaptation (Annicchiarico et al. 2005; Busby et al. 2017; Sauvadet et al. 2021). Likewise, selection of cacao genotypes in more diverse cropping systems such as organic cultivation or agroforestry that harbor and maintain higher microbial diversity (Mäder et al. 2000; Chave et al. 2014; Granzow et al. 2017; Lori et al. 2017; Wang et al. 2017) is likely to accommodate beneficial plant–microbe interactions. However, direct selection of such symbiotic interactions is challenging. A recent EUCARPIA workshop on implementing plant–microbe interactions in plant breeding highlighted the need for new tools and applications, namely high-throughput phenotyping, machine learning and modeling approaches, novel seed treatments and the focus on endophytes, plant genetic markers, gene editing, and monitoring and decision tools for genotype selection in general (Hohmann et al. 2020). Despite the need to close

major knowledge gaps on the relationship between the composition of the root-associated microbiome composition and crop performance and ecosystem services (Finkel et al. 2017; Hartman et al. 2017; Oyserman et al. 2018), certain strategies and tools are available that cacao breeders can use to integrate microbiome functions in breeding programs. For instance, Wille et al. (2020) developed a high-throughput screening system that identifies heritable and field-relevant variation for resistance against conjointly occurring root rot pathogens by incorporating the entire native soil microbiome as a key element of plant resistance. Other studies matched microbial functions with root morphological traits for enhanced water and nutrient uptake (Galindo-Castañeda et al., 2019) and drought and cold tolerance (Orozovic et al. 2019) as a means to directly select symbiosis-efficient plant genotypes in breeding programs. Besides early-stage screening assays, plant selection should occur in target environments in order to incorporate plant–microbe as well as microbe–microbe interactions. Gaue (1998) concluded after years of red clover resistance breeding that selection against multiple soil-borne pathogens was only successful under field conditions. Such approaches allow the selection of cacao genotypes that recruit a disease-suppressive or “healthy” root-associated microbiome, restricting the virulence of predominant pathogens, whereas experiments under axenic conditions alone can overestimate the importance of certain genes (Anderson et al. 2014; Wagner et al. 2016). Furthermore, selection sites can be assessed not only for soil type, soil structure, nutrient content, and pH, but also for soil microbial and rhizosphere communities. Via a comprehensive characterization of the root-associated microbiome, Chang et al. (2017) were able to identify key microbial hubs that successfully predicted soybean productivity. Such characterizations through metagenomic approaches would also enable cacao breeders to make well-informed choices of field sites for selection and variety testing.

We are at the beginning of unraveling the principles of how plant genotypes and their interaction with the native microbiome drive phenotypic variation in disease resistance. Challenges remain. Besides the need to better understand the heritability of microbiome-mediated disease resistance, we need to address the variability of soil microbiomes (including varying pathogen compositions) in different environments. The analysis of functional genotypic variation in microbiome composition will help to identify microbial hubs and key pathogens that play a crucial role in the expression of disease resistance. This information will help to develop novel cacao breeding tools that make efficient use of plant–microbe interactions during the selection process.

3.2.2 Soil carbon sequestration

Carbon (C) storage is a significant regulating service provided within all agroforestry systems (Jose 2009), and microbial processes are key to transforming litterfall and rhizodeposits into stable soil C (Cotrufo et al. 2013; Kallenbach et al. 2016). Within the rhizosphere, microbial community composition influences the fate of soil C and C cycling rates, with shifting patterns of rhizodeposition affecting C use and fixation via the microbial community (Trivedi et al. 2013). The understudied pathway of microbial C use efficiency (CUE), the partitioning of C between microbial biomass and respiration, is strongly controlled by microbial physiology, with higher microbial CUE linked to increased soil C storage (Kallenbach et al. 2019; Saifuddin et al. 2019).

Limited knowledge of the cacao root-associated microbiome means that its contributions to CUE and key C storage patterns in cacao rhizosphere soils remain poorly understood. Nonetheless, it is clear that the integration of shade trees is key to increasing delivery of this regulating service, and the critical role of the root-associated in C sequestration in other systems indicates that this is a microbially mediated strategy. Aboveground and belowground C sequestration in shade trees can increase C storage by fivefold (Abou Rajab et al. 2016). Sauvadet et al. (2020a, b) showed that in cacao agroforestry systems, soil C mineralization was unchanged as compared to a cacao monoculture, but soil C content was either similar or higher depending on shade tree type and traits. Similarly, a meta-analysis of 52 comparisons of agroforestry systems and cacao monoculture found no difference in soil organic carbon (Niether et al. 2020). While no information was available on the microbial communities involved in these studies, such findings do support the need for further investigation into the effects of cacao management on shifts in the core microbiome and subsequent effects on soil C sequestration patterns. Microbial mineralization and transformation of the nutrients contained in litter inputs can additionally reduce the reliance on external inputs to meet cacao nutrient demands, thus contributing a critical supporting service (Fig. 3).

3.3 Supporting services

Supporting services include nutrient and water cycling. Microbial metabolic processes cycle nutrients and alter soil redox conditions, mediating the bioavailability of plant macro- and micronutrients as well as heavy metals of concern for human health. In addition, root-associated microorganisms including mycorrhizae help regulate plant water relations.

3.3.1 Cycling and availability of nutrient resources

Breeding approaches for genotypes adapted to low nutrient availability may enhance root-associated microbiome-mediated pathways for nutrient bioavailability (Rengel and Marschner 2005). Potential nutrient availability in the rhizosphere is controlled by a range of mechanisms including root morphological responses and exudation of organic compounds, which can then alter the abundance and composition of microbial communities. While both indirect (litterfall and decomposition) and direct (external inputs) pathways shape soil nutrient pools in cacao systems (Isaac et al. 2007; Mortimer et al. 2018), microbial activity strongly influences nutrient cycling and bioavailability, suggesting the need to consider the root-associated microbiome in breeding for increased resource use efficiency.

One opportunity to integrate plant and rhizosphere microbial components of resource use efficiency may be for potassium (K). Large amounts of K are required by cacao—around 700 kg ha⁻¹ are required to produce 1 t of seeds per year, with a suggested lower limit of 0.20 meq K 100 g⁻¹ soil based on deficiencies in unshaded cacao (Ahenkorah 1981). Trees with abundant supplies of K are more tolerant to adverse effects of water stress, with an inverse relationship between K dose and leaf transpiration (Orchard 1978). Importantly, cacao cultivars have been observed to differ in their ability to harness non-exchangeable K in the soil, providing the necessary genetic variation for breeding (Wessel 1971). Grapevine rootstocks contrasting in potassium uptake were found to differ in the relative abundance of potassium-solubilizing microorganisms in the rhizosphere (D'Amico et al. 2018). Efforts should be made to understand whether cacao variation in K uptake is similarly linked to the root-associated microbiome (Table 1); if so, understanding the underlying mechanisms could help optimize resource uptake and efficient use of inputs in cacao agroecosystems.

3.3.2 Reduced heavy metal uptake

Using the same principles as for increased resource use efficiency, breeding programs integrating plant and microbial mechanisms could provide a pathway to reduced uptake of heavy metals. Microbial processes partially regulate root uptake of heavy metals by affecting bioavailability of these ions, particularly in the rhizosphere in the topsoil where roots, microorganisms, and metals such as aluminum (Al) and cadmium (Cd) are concentrated (Cañizales-Paredes et al. 2012; Gramlich et al. 2018; Niether et al. 2019).

Cadmium, which can be translocated from soil into cacao beans, is extremely detrimental to human health and has become a topic of interest in cacao due to recently imposed limits on concentrations in chocolate in the European Union. Cacao studies have shown genetic differences and $G \times E \times M$

interactions affecting Cd acquisition and partitioning, but potential links to the root-associated microbiome have been tested only in other crops. Genetic differences among cacao cultivars in Cd uptake from a given soil have been found in a survey of 70 Peruvian cacao plantations (Arévalo-Gardini et al. 2017) and 77 cacao accessions in a genetic library (Lewis et al. 2018), although another study of 11 cultivars at a single site found no genetic effects on rootstock, scion, and leaf Cd concentrations (Engbersen et al. 2019). Allocation of Cd to vegetative and reproductive parts also differs among cultivars and with pod maturation, as shown by greater variability in leaf and bean Cd than in soil Cd (Lewis et al. 2018). A number of mechanisms could be responsible for cacao variation in Cd uptake (e.g., differences in root system size or morphology, transporter kinetics, microbial interactions, or root exudation of metal-chelating compounds (Lewis et al. 2018)) and partitioning (e.g., xylem-to-phloem loading of Cd during bean maturation (Engbersen et al. 2019)). Grafting may help reduce Cd uptake, though more research is needed. In one study, CCN51 had 50% lower leaf Cd content when grown on its own rootstock than when grafted onto rootstock obtained from hybrids of CCN51 and ICS95 (Arévalo-Gardini et al. 2017).

Root exudates deserve further study as a potential breeding target to manipulate Cd availability in the rhizosphere, either directly or indirectly via microbial recruitment (Table 1). Many plant species alter the quality and/or quantity of root exudates upon exposure to heavy metals (Bali et al. 2020), potentially increasing or decreasing Cd bioavailability depending on the compounds involved (Luo et al. 2014). It was recently demonstrated that strigolactones, a class of plant hormones key to mediating abiotic stresses such as drought and salinity (Saeed et al. 2017), could be exogenously applied to promote endogenous production, effectively reducing Cd uptake and accumulation in switchgrass seedlings (Tai et al. 2017). In addition, exudates may provide a mechanism to recruit beneficial microbial taxa that reduce heavy metal bioavailability.

Aluminum (Al) toxicity and responses in cacao represent an important but understudied topic (de Almeida et al. 2015), as Al toxicity limits agricultural productivity in roughly half of the arable land in cacao-producing regions (Ahenkorah 1981). Al toxicity reduces the plant's ability to extract water and nutrients from the soil, and in conditions of low pH such as most tropical soils, Al is dissolved and becomes toxic to many plants including cacao (Borém et al. 2012). In a small study, two genotypes (Catongo and Theobahia) showed significant differences in their tolerance to Al phytotoxicity, with Theobahia responding with higher growth and improved mineral nutrition (Ribeiro et al. 2013). Al uptake and exclusion should be assessed in more varieties to determine variation in aluminum tolerance and the potential for breeding in cacao.

Arbuscular mycorrhizal fungi (AMF), important symbionts of cacao and many other plant species, have been shown to alleviate Cd and Al toxicity via mechanisms that reduce their activity and translocation to shoots (Seguel et al. 2013; Rufyikiri et al. 2000; Cui et al. 2019; Chen et al. 2004; Rask et al. 2019). Microbial processes regulate bioavailability of metals such as Cd and Al through effects on the soil physicochemical environment: altering pH or metal ion valency; directly binding the ions; synthesizing organic compounds that solubilize or sequester metal ions; or in the case of cadmium, producing H_2S to form an insoluble CdS precipitate (Bali et al. 2020). Alternatively, microorganisms can also affect heavy metal uptake through root-related mechanisms such as increasing root surface area or increasing transfer of ions from the rhizosphere into the plant (Sessitsch et al. 2013). Augmentation of heavy metal-chelating bacteria is being explored to reduce Cd and Al uptake and toxicity in other crops (Panhwar et al. 2015; Mora et al. 2017; Dutta and Bora 2019; Zeng et al. 2020). Breeding cacao varieties to recruit beneficial Cd- and Al-chelating microorganisms could complement plant-mediated tolerance mechanisms.

3.3.3 Water relations

Favorable microclimate modifications provided by the integration of shade trees affect water relations (regulating service; Fig. 3). Cacao yield is highly sensitive to the timing and degree of water deficits (Moser et al. 2010). Recent models suggest that water stress will become increasingly important for cacao production as the climate in growing regions is predicted to significantly change (Schroth et al. 2016), although the impacts of water stress will not be evenly distributed due to seasonal and regional variability in precipitation patterns under climate change (Black et al. 2020). The effect of shade trees on cacao water stress varies depending on soil moisture availability: shade trees can exacerbate water stress via increased competition in dry soils or alleviate water stress through reduced evapotranspiration in shaded cacao (Somarriba et al. 2018). Niether et al. (2020) found 1.7% lower soil volumetric water content and more moderate temperatures in agroforestry systems as compared to cacao monocultures, highlighting the strong impact of shade trees on the soil microenvironment and consequent impacts on water-related supporting services.

Recent studies suggest that cacao adapts to water deficits via changes in morphology and growth patterns (Lahive et al. 2019; Borden et al. 2020) and that these differences in cacao root morphology in response to water deficits are genotype-specific (dos Santos et al. 2014). Broadly, changes in root morphology, carbon deposition, and root exudates are stimulated under water stress, which can then alter soil

microorganism composition (Hartman and Tringe 2019). The root-associated microbiome provides water-related supporting services and confers abiotic stress tolerance during and after drought via complex feedbacks (De Vries et al. 2020), which are highly dependent on soil C chemistry (Bhattacharjee et al. 2020). Yet no work to date has documented the role of this root response to water stress on rhizosphere microbial communities nor the role of the cacao root-associated microbiome in conferring resilience under water deficits.

4 Challenges and future perspectives

With so much potential to increase the ecosystem services associated with cacao production, it is perhaps surprising that so many questions about the cacao root-associated microbiome remain unanswered. The long timeframes involved in perennial breeding have constrained understanding of plant–microbe interactions in agroforestry systems, but recent advances in molecular methods could help accelerate breeding cycles. The broad geographic range of *T. cacao* and diverse, decentralized smallholder farms that produce the majority of the world's cacao may have presented logistical barriers for sampling. Cacao production often occurs on small farms that may limit the feasibility of large numbers of replicates, for example. In the context of this variation, efforts to identify and augment beneficial taxa should be conducted at the local scale, ideally within a participatory framework that capitalizes on native soil microbial communities to address production challenges of greatest concern to local farmers. Establishment of long-term research trials in multiple agroecological zones would also be of great benefit for knowledge transfer across regions, particularly in the context of climate change and adaptation. Rapid breeding strategies and locally focused research combined with global knowledge transfer could help optimize the natural capital of the cacao root-associated microbiome, alleviating reliance on external inputs and increasing the sustainability of cacao production in the future.

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