PLANT DISEASE FEATURE

Tree Effects on Coffee Leaf Rust at Field and Landscape Scales

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Abstract

Although integrating trees into agricultural systems (i.e., agroforestry systems) provides many valuable ecosystem services, the trees can also interact with plant diseases. We demonstrate that a detailed understanding of how plant diseases interact with trees in agroforestry systems is necessary to identify key tree canopy characteristics, leaf traits, spatial arrangements, and management options that can help control plant diseases at different spatial scales. We focus our analysis on how trees affect coffee leaf rust, a major disease affecting one of the world's most significant crop commodities. We show that trees can both promote and discourage the development of coffee leaf rust at the plot scale via microclimate modifications in the understory. Based on our understanding of the role of tree characteristics in shaping the microclimate, we identify several canopy characteristics and leaf traits that can help manage coffee leaf rust at the plot scale: namely, thin canopies with high openness, short base height, horizontal branching, and small, dentate leaves. In contrast, at the edge of coffee farms, having large trees with high canopy volume and small, thick, waxy leaves is more useful to reduce throughflow wind speeds and intercept the airborne dispersal of urediniospores, an important consideration to control disease at the landscape scale. Seasonal pruning can help shape trees into the desired form, and trees can be spatially arranged to optimize desired effects. This case study demonstrates the added value of combining process-based epidemiology studies with functional trait ecology to improve disease management in agroforestry systems.

Keywords: agroforestry, disease ecology, functional trait ecology, *Hemileia vastatrix*, microclimate, process-based models, traits, tree management

Coffee is a shade-adapted plant (Cannell 1985; DaMatta 2004), which is commonly grown in integrated agroforestry systems (i.e., the intercropping of coffee and trees within a farm) (Fig. 1). Growing coffee in agroforestry systems is a traditional farming practice that remains the dominant mode of coffee production in many parts of the world, including in most Latin American countries (Jha et al. 2014). The trees can provide a wide range of ecosystem services from the local to landscape scales, including carbon sequestration, nutrient capture and cycling, soil amelioration, coffee yield stability, provision of additional food products, and microclimate regulation (Isaac and Borden 2019; Meylan et al. 2017; Vaast et al. 2016). These ecosystem services provided by trees can improve coffee's resilience to abiotic stress such as climate change (Lasco et al. 2014); however, their effect on biotic stresses such as those caused by prevalent coffee diseases is still poorly understood. This is problematic, given that major coffee diseases continue to cause significant yield loss around the world. Coffee leaf rust, caused by *Hemileia vastatrix*, is one of the most important coffee diseases (Avelino et al. 2018), having recently caused severe epidemics in Colombia, Central America, Mexico, the Caribbean, Peru, and Ecuador (Avelino et al. 2015; McCook and Vandermeer 2015).

The difficulties in understanding tree effects on coffee diseases, and especially coffee leaf rust, arise from the inherent complexity of agroforestry systems, because trees can have interacting, and often contradictory, effects on disease development. For example, trees can modify the microclimate in ways that both favor pathogen development and simultaneously promote coffee plant physiological resistance (Schroth et al. 2000) (Table 1). Furthermore, although some work on coffee diseases integrates characteristics of agroforestry systems such as shade tree cover (i.e., the extent of shading provided by the shade tree canopy) (Avelino et al. 2012) or the number of canopy strata (i.e., the vertical layering of shade tree canopy (Soto-Pinto et al. 2002), most studies on coffee agroforestry systems have focused on a dichotomy comparing them to unshaded monocultures (Fig. 1). In doing so, the defining characteristics of tree canopies and their leaves are ignored and the inherent differences

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between agroforestry systems are omitted from research questions (Gagliardi et al. 2021). This omission occurs despite the inter- and intraspecific variability of tree traits (Gagliardi et al. 2021; Hallé et al. 1978). It is further confounded by the many management possibilities controlling tree spatial arrangements (vertical canopy strata and horizontal positioning), planting densities of trees, and degree of shade cover (Fig. 2). We know that these differences between agroforestry systems interact with regionally specific macroclimatic and edaphic

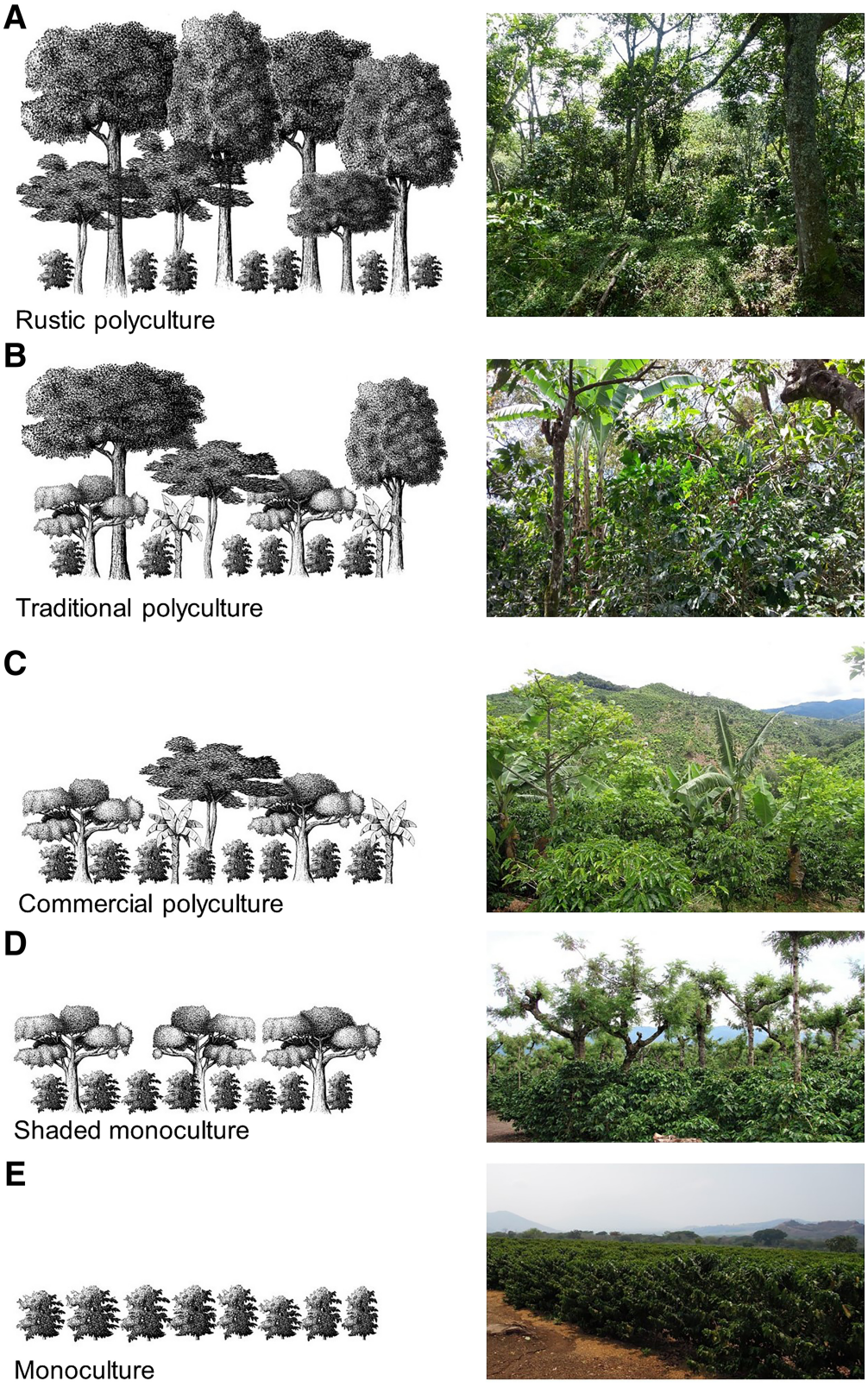

Fig. 1. Illustrations and photographs of the range of coffee system structures, ranging from agroforestry systems (including rustic polycultures, traditional polycultures, commercial polycultures and shaded monocultures) to unshaded monocultures. Descriptions and illustrations based on Moguel and Toledo (1999). Photographs courtesy of **A,** Bruno Rapidel; **B,** Clémentine Allinne; and **C, D, and E,** Jacques Avelino. Drawings by Stephanie Gagliardi.

conditions in unique ways (Gagliardi et al. 2022; van Oijen et al. 2010), creating unique understory conditions, and, therefore, directly and indirectly affect disease development.

In this article, we combine detailed knowledge of the factors driving coffee disease development with the interacting and complex effects of trees in agroforestry systems and landscapes to identify key tree traits and management opportunities to help control coffee disease. Focusing on coffee leaf rust as a model coffee disease, given its global prominence and economic impacts, we draw on experimental and observational studies from Latin America, notably in Costa Rica and Mexico, as well as other coffee-producing regions, including Uganda and Ethiopia. We begin with a more detailed overview of coffee-based agroforestry systems and the complexity of coffee disease within them. We then present each stage of coffee leaf rust development to better understand how disease pathways are stimulated by trees. We end our article with a proposed tree typology, with key canopy characteristics and leaf traits, tree spatial arrangements, and tree management options, that can be integrated into disease management practices to help control coffee leaf rust at various life cycle

Table 1. Tree effects on coffee diseases

Common name	Scientific name	Pathways involved	References
American leaf spot disease of coffee	*Mycena citricolor*	Alternate host for the pathogen	Sequeira 1958[a]; Waller et al. 2007[a]
	–	Microclimate modifications affecting the pathogen	Avelino et al. 2007[a]; Cerdán et al. 2012[a]; Schroth et al. 2000[a]
Armillaria root rot	*Armillaria* spp.	Alternate host for the pathogen	Waller et al. 2007[a]
Pink disease	*Corticium salmonicolor*	Alternate host for the pathogen	Roux and Coetzee 2005[a]; Waller et al. 2007[a]
	–	Microclimate modifications affecting the pathogen	Schroth et al. 2000[a]; Waller et al. 2007[a]
Thread blight	*Corticium koleroga*	Alternate host for the pathogen	Benchimol et al. 2001[a]; Waller et al. 2007[a]
	–	Microclimate modifications affecting the pathogen	Belachew et al. 2015[a]; Schroth et al. 2000[a]; Waller et al. 2007[a]
Coffee leaf scorch	*Xylella fastidiosa*	Alternate host for the pathogen or vector	Brodbeck et al. 2017[a]; Sicard et al. 2018[a]
Brown eye spot	*Cercospora coffeicola*	Microclimate modifications affecting the pathogen	Echandi 1969[b]; Goulart da Silva et al. 2016[b]
Dieback syndrome	*Colletotrichum* spp.	Microclimate modifications affecting the coffee plant	Muller et al. 2004[b]
Phoma leaf blight	*Phoma costarricensis*	Microclimate modifications affecting the coffee plant	Muller et al. 2004[b]
Coffee berry disease	*Colletotrichum kahawae*	Microclimate modifications affecting the pathogen	Bedimo et al. 2008[b]; Waller et al. 2007[a]
Coffee leaf rust	*Hemileia vastatrix*	Microclimate modifications affecting the pathogen	Avelino et al. 2020[a]; Boudrot et al. 2016[c]; Gagliardi et al. 2020[a]; Liebig et al. 2019[c]; Lopez-Bravo et al. 2012[a]
	–	Microclimate modifications affecting the coffee plant	Eskes 1982[b]; Lopez-Bravo et al. 2012[a]
	–	Microclimate modifications affecting antagonists	Galvão and Bettiol 2014[b]
	–	Modified habitat affecting antagonists	Vandermeer et al. 2009[b]

[a] Reference indicates a favorable effect on pathogens.
[b] Reference indicates a negative effect on pathogens.
[c] Reference indicates opposite effects, negative and positive, that can result from interactions.

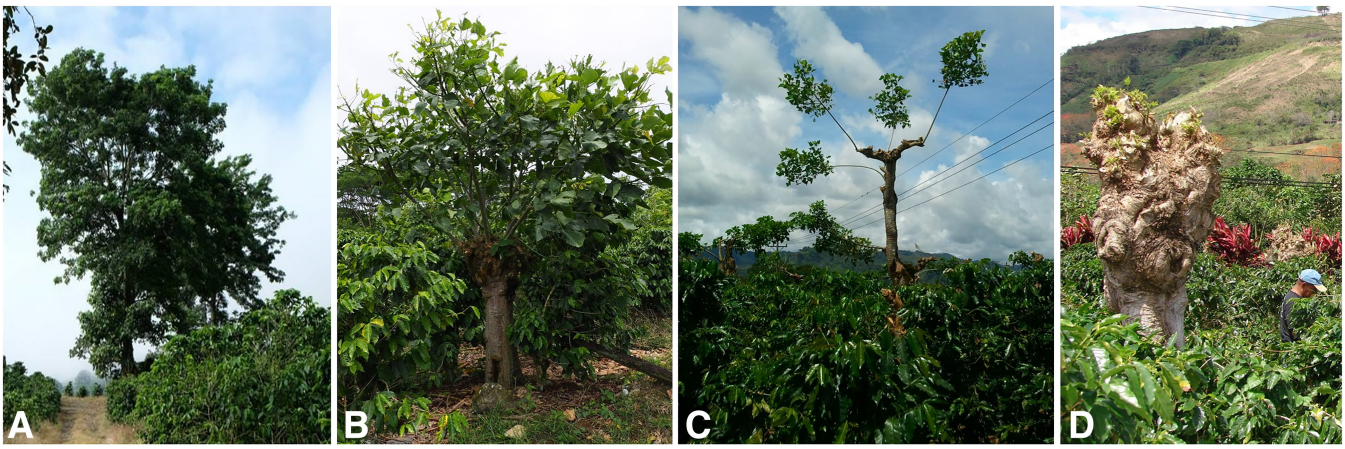

Fig. 2. Gradient of shade cover provided by a single tree species, *Erythrina poeppigiana*, due to a variety of tree management practices and timing since pruning. **A,** No pruning management, free growth; **B,** 8 to 10 months after severe pruning; **C,** severe pruning with select branches maintained; and **D,** severe pruning with no branches maintained. Photographs courtesy of Serra Buchanan (A), Stephanie Gagliardi (B and C), and Jacques Avelino (D).

stages. We demonstrate how process-based epidemiology studies can be combined with functional trait ecology to improve disease management in coffee-based agroforestry systems.

An Overview of Coffee Agroforestry Systems

Coffee farms vary in their plant biodiversity and structure, with a range of tree spatial distributions both vertically (i.e., canopy strata) and horizontally (i.e., planting arrangement), as well as in tree canopy density and shade cover. Moguel and Toledo (1999) characterized coffee-based agroforestry systems according to tree canopy strata, ranging from unshaded, sun-exposed coffee monoculture (no tree strata), shaded monoculture coffee (low canopy heights of a single tree species), and commercial polyculture (tree canopies of low- to medium-height with two strata) to traditional polyculture and rustic systems (tall tree canopies with three strata) (Fig. 1). As reported in cacao systems (Gidoin et al. 2014), tree spatial arrangements in integrated agroforestry systems can vary as a function of farmer management decisions, where trees tend to be (i) aggregated when they grow due to natural regeneration with few farmers' interventions, (ii) randomly distributed when farmers remove some naturally regenerating trees and plant new trees based on preference, and (iii) evenly distributed when tree spatial arrangements are preplanned during plantation establishment, especially in shaded monocultures. Although most published studies are from the Americas, in particular Mesoamerica (Cerdán et al. 2012; López-Gómez et al. 2008; Valencia et al. 2014), there is growing literature from Africa (Negawo and Beyene 2017) and Asia (Devagiri et al. 2020) that shows similar variability among coffee-based agroforestry systems (Supplementary Table S1).

There is a wide range of tree species richness across coffee-based agroforestry systems that often contain a high percentage of native tree species (Valencia et al. 2014). However, most coffee-based agroforestry systems tend to be dominated by a few tree species that are favored by farmers, often because they are nitrogen-fixing, easy to prune, or have some commercial value (e.g., timber or fruit). Trees also differ inter- and intraspecifically (Gagliardi et al. 2020; Hallé et al. 1978) in their phenology, canopy characteristics (e.g., canopy size and openness), leaf traits (e.g., leaf area and leaf texture), and rooting patterns (e.g., rooting depth). This diversity of characteristics is often directly managed by farmers (i.e., via pruning) to enhance the productivity and sustainability of the coffee system as a whole (Cerdán et al. 2012; Isaac et al. 2018).

Coffee Diseases in Agroforestry Systems

Coffee diseases are influenced by trees at the plot scale, at the edge of farms, and at the larger landscape scale via direct and indirect effects. More specifically, trees can directly affect diseases by affecting the pathogen via interactions with the macroclimate, in turn modifying the microclimate in their understory or intercepting wind at an even larger scale. On the other hand, trees can have indirect impacts on diseases by creating favorable environments for pathogen antagonists and by affecting the physiology of the host plant, either through habitat conservation, microclimate modifications, or changes to the chemical and physical characteristics of the soil (Ratnadass et al. 2012; Schroth et al. 2000).

Despite the diversity of structures and composition of characteristics possible in coffee-based agroforestry systems, some coffee pathogens seem to consistently prefer either agroforestry systems or unshaded monocultures (Table 1). This seems to be the case for secondary pathogens that have likely not been studied in depth. For instance, some multihost fungal pathogens such as *Mycena citricolor*, causal agent of American leaf spot disease; *Corticium koleroga*, causal agent of thread blight; and *C. salmonicolor*, causal agent of pink disease have been consistently reported to prefer agroforestry systems, hypothetically due to longer foliar wetness duration (Avelino et al. 2007; Belachew et al. 2015; Cerdán et al. 2012; Schroth et al. 2000; Waller et al. 2007), and the availability of more plant hosts, including some tree species commonly used in coffee-based agroforestry systems (Benchimol et al. 2001; Roux and Coetzee 2005; Sequeira 1958; Waller et al. 2007). Similarly, *Armillaria* spp. (root rot) (Waller et al. 2007), and *Xylella fastidiosa* (coffee leaf scorch) and its vectors (Brodbeck et al. 2017; Sicard et al. 2018) have a large host range and should prefer the greater plant biodiversity of agroforestry systems. In contrast, other pathogens prefer unshaded monoculture conditions. For example, *Cercospora coffeicola* (brown eye spot) is favored by high air temperatures and light exposure (Echandi 1969; Goulart da Silva et al. 2016), while dieback syndrome, exacerbated by the presence of *Colletotrichum* spp., is favored by nutritional disequilibria of the coffee plant (Muller et al. 2004), all conditions that are characteristic of unshaded monocultures relative to agroforestry systems, regardless of geographic location. Similarly, *Phoma costarricensis* (leaf blight) prefers exposed, unshaded coffee plots, where strong winds are unimpeded, provoking wounds in young coffee leaves and providing entry points for the fungal pathogen (Muller et al. 2004).

For some coffee diseases, however, tree effects can be unclear (Table 1). For example, there are contradictions in the literature concerning tree effects on the coffee berry disease, caused by *Colletotrichum kahawae*. For instance, overstory trees can promote raindrop interception, reducing throughfall amounts and subsequent splash dispersal of conidia, which has led to reports of reduced coffee berry disease incidence in the understory of trees (Bedimo et al. 2008). Simultaneously, trees can prolong coffee berry wetness duration, which has led to reports of increased coffee berry disease incidence in the understory (Waller et al. 2007).

Tree effects on coffee leaf rust, caused by *H. vastatrix*, are similarly complex and often contradictory, because they can (i) affect the pathogen, the host plant, or antagonist species; (ii) occur via microclimate modifications by interacting with larger scale macroclimate conditions and other habitat modifications; and (iii) be positive or negative depending on the pathway involved. Our lack of understanding of how trees in agroforestry systems affect coffee diseases possibly denotes a lack of knowledge about the disease epidemiology or disease interactions with the fluctuating conditions in the agroforest understory. To explore this complexity, we use coffee leaf rust as model coffee disease to describe the complex effects of trees in agroforestry systems specific to each life cycle stage in the following sections.

H. vastatrix Life Cycle and the Role of Trees

H. vastatrix is an obligate parasite of coffee. This biotrophic fungus has caused heavy yield losses, particularly since 2008 in Latin America, due to a combination of favorable regional meteorological

Fig. 3. Impact of coffee leaf rust on a susceptible coffee cultivar in a Costa Rican commercial plot after the intense epidemics that hit Central America from 2012. Photograph courtesy of Jacques Avelino.

conditions and difficult economic factors that both contributed to suboptimal coffee crop management (Avelino et al. 2015). Coffee leaf rust causes primary losses due to defoliation (Fig. 3), which results in berry decay, and lower coffee quality if berries of defoliated branches are harvested. Coffee leaf rust also causes secondary losses (i.e., in years following an epidemic) due to the death of heavily defoliated branches that no longer produce berries.

The first symptoms of the disease are minute, light-yellow lesions on the abaxial side of infected coffee leaves (Fig. 4A). These lesions grow and start to produce orange spores covering almost the whole lesion surface, except the surrounding area corresponding to lesion margins (Fig. 4B and C). When lesions grow, they coalesce (Fig. 4C). Ultimately, the lesions become necrotic, starting from the center where infection initiated (Fig. 4D).

The only spore that contributes to epidemic growth is the urediniospore, resulting from either asexual multiplication or cryptosexuality (Carvalho et al. 2011). Teliospores can also be found sporadically in lesions; they germinate and produce basidiospores that cannot infect coffee. Many factors affect the *H. vastatrix* life cycle at different stages (Fig. 5), including abiotic factors (e.g., light, wind, temperature, rain, and soil moisture), host characteristics (e.g., fruit load and genetic resistance), as well as other biological factors (e.g., antagonist species). Excluding complete genetic resistance (i.e., vertical resistance) driven by a gene-for-gene relationship (Flor 1971), all of these factors are influenced by trees in distinct ways, where their overall effect is the accumulation of both positive and negative effects on the disease (Table 2). We hypothesize that there are tree typologies, relevant spatial scales of intervention, and management practices that can help reduce specific adverse effects of trees on disease management. However, a deeper understanding of tree effects is needed. In the following sections, we describe the factors driving each life cycle stage of *H. vastatrix* and outline how trees affect each stage, as reported in the literature, to then deduce the main pathways involved.

Infection

The infection process can be completed quickly, in less than 6 h, and involves two main subprocesses: urediniospore germination and penetration via stomata on the abaxial side of the leaf. Infection is enhanced in darkness and requires the presence of free water (Rayner 1961a). Temperature requirements are more complex. Germination is optimal at 22 to 23°C, whereas the growth of the germ tube is stimulated at 17°C, and appressorium formation above a stoma, just before penetration, is fastest at 13 to 16°C (De Jong et al. 1987). Germination nearly ceases when temperatures drop too low (approximately 10°C) or rise too high (approximately 31°C) (De Jong et al. 1987). In the tropics, microclimatic conditions ideal for infection may frequently occur at dawn, as temperatures often decrease to their minimum, promoting appressorium formation, and the morning dew can provide the wetness needed for penetration.

Additionally, infection depends on leaf receptivity to *H. vastatrix* (i.e., level of susceptibility to the pathogen independent of genetic resistance) (Richard et al. 2012), which can be modified by several poorly understood factors. For example, the fruiting load of the coffee branch seems to affect the success of the infection process, because Eskes and de Souza (1981) found 34% more lesions on inoculated leaf disks from productive branches compared with branches with no berry production, potentially due to the allocation of defensive phenolic compounds away from leaves to maturing berries (de Carvalho et al. 2001). Similarly, Hoogstraten et al. (1983) found 6.7 times more lesions on inoculated leaves when soil moisture was high compared with low soil moisture conditions, possibly due to greater stomatal opening when humidity is high (Tesha and Kumar 1978), though penetration does not require stomata to be open, because penetrating hyphae exert enough pressure to bypass stomatal guard cells (Talhinhas et al. 2014).

Although there are no specific studies on the effects of trees on the infection process, we know that shade cover can affect a variety of the conditions listed above. For example, shade cover reduces solar radiation levels and moderates the diurnal temperature range in the understory, mitigating temperature extremes (Gagliardi et al. 2021; Liebig et al. 2019; López-Bravo et al. 2012; Merle et al. 2022; Siles et al. 2010a), especially at high altitudes where minimum temperatures are generally lower (Liebig et al. 2019). However, the extent of this moderation effect depends on seasonal and macroclimatic conditions. Shade cover also complicates leaf wetness dynamics, where it can (i) prolong leaf wetness duration by preventing evaporation from wet leaf surfaces (López-Bravo et al. 2012), especially in rainy locations where relative humidity can remain high in the understory of trees (Liebig et al. 2019); or (ii) prevent initial leaf wetting, either by preventing dew formation (Merle et al. 2022), especially in drier, high altitude locations (Liebig et al. 2019), or from reducing overall throughfall amounts (Avelino et al. 2020).

Shade cover and the resulting decrease in solar radiation indirectly affect the infection process by reducing leaf receptivity to *H. vastatrix* via leaf physiological changes and a reduction in the coffee plant fruiting load (Eskes and de Souza 1981). This variability

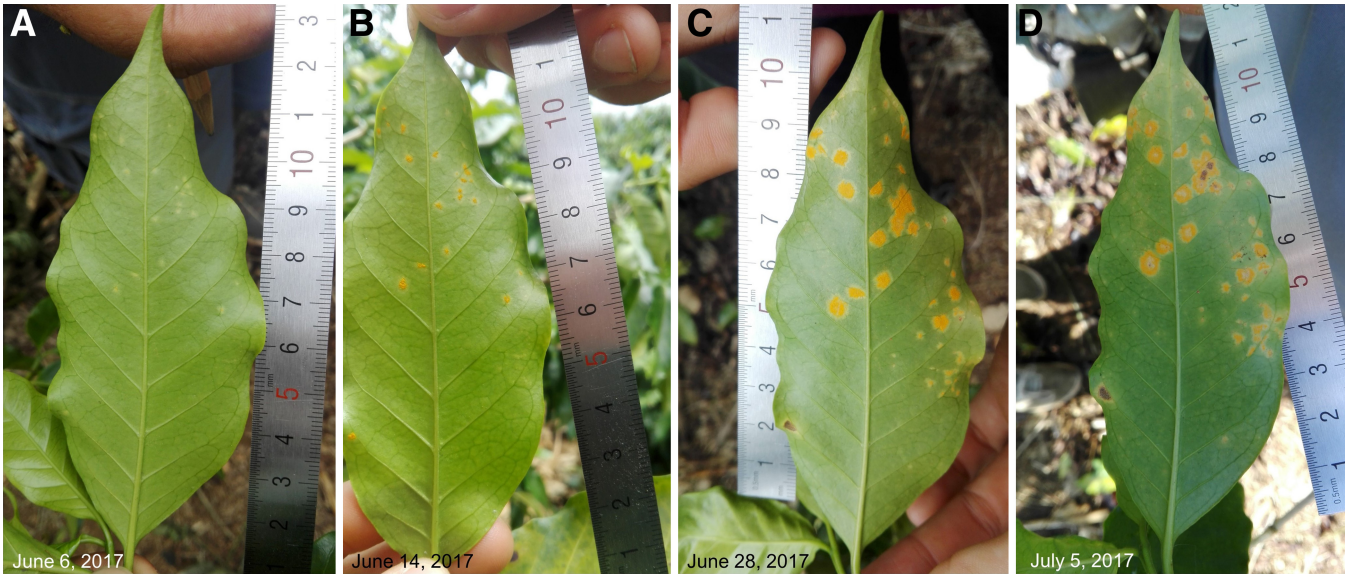

Fig. 4. Symptoms and signs of coffee leaf rust (*Hemileia vastatrix*). **A,** Initial chlorotic lesions; **B,** initial sporulation with orange urediniospores; B, **C, and D,** sporulation and well-defined yellowish lesion margin; and C and D, coalescence of growing lesions and necrotic lesions. Photographs courtesy of Steven Cerdas.

is reflected in studies assessing plant-level coffee leaf rust incidence in Central America, which is often higher under trees compared with unshaded monocultures (López-Bravo et al. 2012; Staver et al. 2001), but can also decrease as the number of tree strata (Soto-Pinto et al. 2002) and shade cover increases (Gagliardi et al. 2021; Zewdie et al. 2021). These trends are further complicated by a location's altitude (Liebig et al. 2019) and geographic location, because trees interact with regional climate dynamics in unique ways.

Colonization

Once *H. vastatrix* is inside the leaf, temperature is the main abiotic factor that affects leaf colonization. Leaf receptivity, which is influenced by leaf physiology, is another theoretical factor affecting colonization. However, to our knowledge, there is no clear information on how these factors specifically affect lesion expansion. Nonetheless, there is information on the latent period (i.e., the time elapsed from infection to the emergence of the first propagules), which reflects a period of leaf tissue colonization. If we assume that rapid production of urediniospores is positively linked to rapid lesion expansion (Gil Fagioli et al. 1990), then conditions that shorten the latent period will also promote lesion expansion. Waller (1982) mentioned that the latent period is shortest (2 weeks) when temperatures range from 22 to 28°C. Although we know that temperatures are moderated by shade cover, this moderation would ideally create temperatures that suit the optimal range of coffee plants (18 to 26°C, depending on coffee species) (DaMatta 2004), which would also be within the optimal range for the *H. vastatrix* colonization process.

Similar to the infection process described above, the latent period is affected by fruit load, light exposure, and soil moisture, though these effects appear limited. Eskes and de Souza (1981) found that the latent period in Brazil was shortened by 12% in leaves from high-

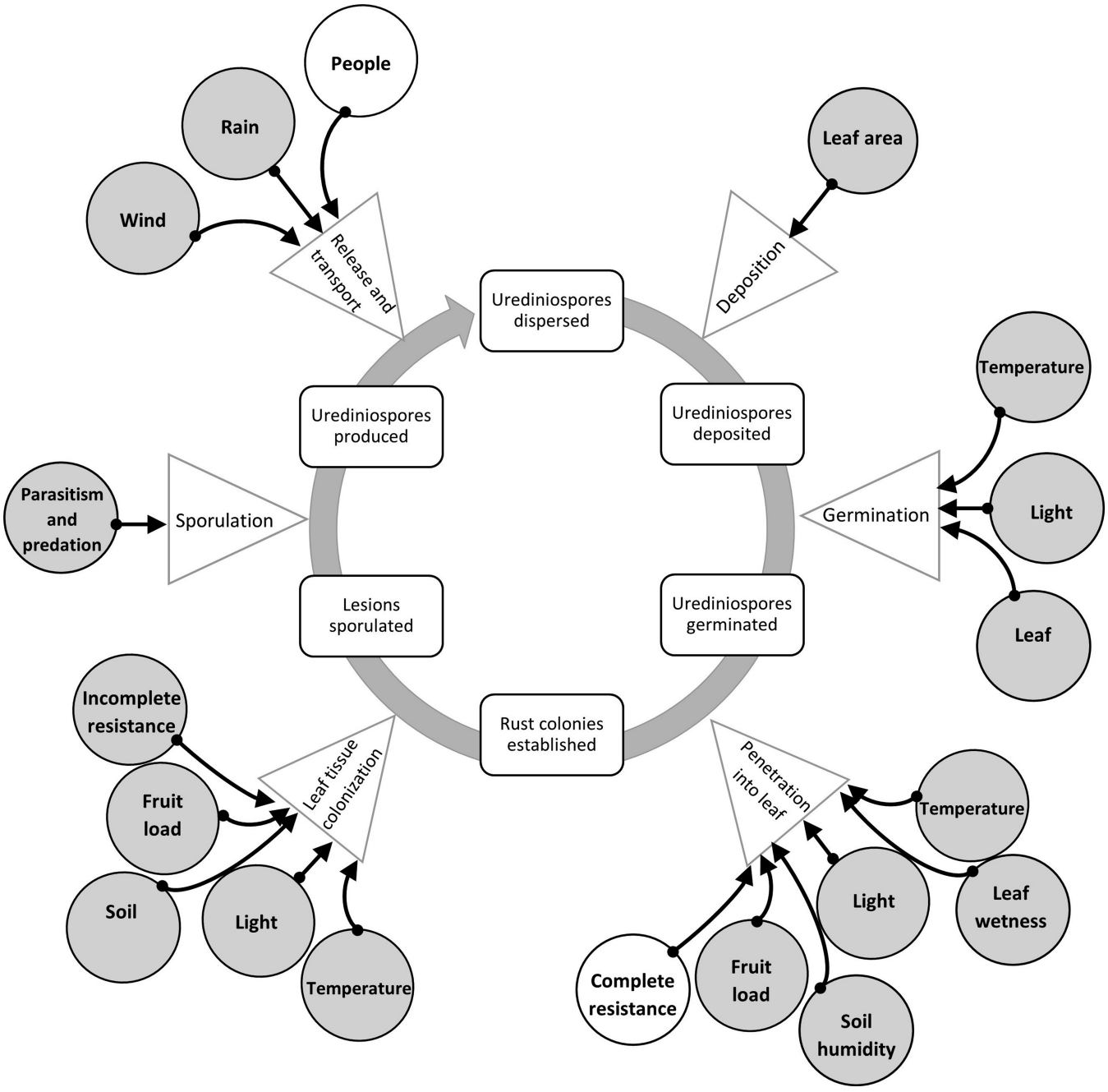

Fig. 5. *Hemileia vastatrix* life cycle and main influencing factors. Rectangles = state variables, triangles = processes or subprocesses, and circles = factors. Shaded circles are factors under the influence of trees in the plot or in the landscape. Modified from Avelino et al. (2004).

yielding branches compared with leaves from branches with no berry production. In unproductive plants, low light intensity (24% of total radiation) and high soil moisture (approximately 33%) reduced the latent period by only 13 and 15%, respectively, relative to total radiation (2,200 J cm^{-2}) and low soil moisture (approximately 12 to 22%) (Eskes 1982; Hoogstraten et al. 1983). This minimal reduction of the latent period as related to light conditions was also observed by de Moraes et al. (1976) and Leguizamón-Caycedo et al. (1998), who compared shaded and unshaded young and unproductive coffee plants at various altitudes in a coffee-producing region of Colombia.

We can also use coffee leaf rust severity (i.e., the relative proportion of diseased leaf area) to reflect, at least in part, the colonization process, because it is partially determined by lesion expansion. When we consider coffee leaf rust severity, we continue to see a minimal effect from shade cover (López-Bravo et al. 2012; Merle et al. 2020a). For example, the greater shade cover provided by two overlapping canopy strata, *Erythrina poeppigiana* and *Chloroleucon eurycyclum*, induced only a slight increase in coffee leaf rust severity (Merle et al. 2020a), whereas lower shade cover provided by a single tree species, *E. poeppigiana*, had no effect compared with unshaded conditions (López-Bravo et al. 2012; Merle et al. 2020a).

Sporulation

Sporulation occurs through the stomata on the abaxial side of coffee leaves. Temperature and relative humidity are hypothesized to indirectly affect sporulation by regulating stomatal opening in coffee leaves (Tesha and Kumar 1978), which facilitates the release of urediniospores (Guggenheim and Harr 1978). In the literature, we find evidence supporting this hypothesis. For example, a positive relationship was observed between disease intensity and soil moisture (Hoogstraten et al. 1983). In addition, Merle et al. (2020b) identified a quadratic relationship between the daily maximum air temperature (up to approximately 30°C) and the growth of the spore-bearing surface of individual lesions, and a negative relationship with daily leaf temperature range, possibly related to stomatal closure at high temperatures. These abiotic conditions are strongly influenced by shade cover, as has been previously discussed, where shade cover interacts with macroclimatic conditions to moderate temperature extremes.

The number of urediniospores and their viability is also highly dependent on the presence of antagonist species such as the hyperparasite fungi *Lecanicillium lecanii* and *Simplicillium* spp. (Fig. 6A) and insect predator *Mycodiplosis hemileiae* (Fig. 6B), a fly whose larvae feed on the urediniospores (Hajian-Forooshani et al. 2016; James et al. 2016). These antagonist species can be affected by trees. For example, shade cover reduces light intensity, which promotes *L. lecanii*, a fungus that is particularly sensitive to UV-B radiation (Galvão and Bettiol 2014). Trees can also support more complex ecological webs such as the mutualistic relationship between ants (*Azteca sericeasur*) and scales (*Coccus viridis*) identified in Mexico,

Table 2. Plausible tree effects on coffee leaf rust and involved pathways[a]

Effects	Infection	Colonization	Sporulation	Dispersal
On *Hemileia vastatrix*				
Buffered temperatures	+	0	0	0
Reduced radiation	+	0	0	0
Increased leaf wetness duration	+	0	0	0
Reduced dew	−	0	0	0
Increased raindrop kinetic energy	0	0	0	+
Reduced throughfall amounts	0	0	0	+
Reduced wind speeds	0	0	0	−
On *Coffea arabica*				
Reduced fruit load	−	−	0	0
Direct decrease of leaf receptivity	−	−	0	0
Longer stomatal opening	0	0	+	0
On antagonist species				
Reduced light and increased wetness	0	0	−	0
Trees as habitats for ants	0	0	−	0

[a] Symbols: + indicates favorable effect, 0 indicates insignificant or no effect, and − indicates adverse effect.

Fig. 6. A, *Lecanicillium lecanii* parasitizing and **B,** *Mycodiplosis hemileia* larvae feeding on *Hemileia vastatrix* urediniospores. Photographs courtesy of Bruno Rapidel.

because trees can provide nesting sites for *A. instabiliz*. When scale populations increase, they become more vulnerable to *L. lecanii*, which is also an entomopathogenic fungus (Vandermeer et al. 2009). In turn, populations of *L. lecanii* increase and contribute to regulating *H. vastatrix* (Jackson et al. 2012). This complex web, however, does not appear to be consistent across regions, because it has not been identified in other coffee-producing regions, including Puerto Rico (Hajian-Forooshani et al. 2016) and Ethiopia (Zewdie et al. 2021).

Dispersal

The dispersal process of mature urediniospores involves three subprocesses: urediniospore release, transport to new host material, and deposition on the underside of coffee leaves. The main abiotic factors responsible for urediniospore release are rainfall events and wind action; more specifically, the impact of raindrops vibrating coffee leaves, the wetting of sporulating lesions, and the turbulence around coffee leaves created by wind action that releases clusters of urediniospores (Nutman et al. 1960; Rayner 1961b). Once released, urediniospores are predominantly transported again by rain and wind, where raindrop movement on the leaf surface or raindrop splashing can transport urediniospores over short distances (i.e., within the same coffee leaf or coffee plant) (Fig. 7) (Bock 1962; Nutman et al. 1960; Rayner 1961b), and wind can transport urediniospores over medium to large distances (i.e., within farms or across landscapes and oceans) (Becker and Kranz 1977; Bowden et al. 1971). Of these two abiotic factors, urediniospores are dispersed primarily by wind, especially during dry conditions, and to a lesser extent by rain (Becker and Kranz 1977). However, released urediniospores are particularly vulnerable to wash-off by rains that carry them to the ground, eliminating a considerable proportion of the viable inoculum stock (Avelino et al. 2020). Urediniospores can also be transported by insects, though there are limited reports describing this mechanism, and by people, especially during harvest, when human movement within coffee plantations peaks (Becker and Kranz 1977).

Trees directly interact with both rainfall events and wind action on several scales. At the plot scale, trees interact with rainfall by (i) redirecting part of the flow of raindrops along their branches and down their main stem, thus promoting stemflow; and (ii) accumulating raindrops on their leaves, thus encouraging canopy storage (Schroth et al. 1999). These interactions with rainfall have important implications for the dispersal of *H. vastatrix* urediniospores. First, by promoting stemflow and canopy storage, the amount of throughfall that reaches the understory is limited (Schroth et al. 1999), which then prevents urediniospore wash-off from sporulating lesions, in turn maintaining the viable inoculum stock in plots (Avelino et al. 2020). This interaction with throughfall seems to favor coffee leaf rust epidemic development at the plot scale. The accumulation of raindrops in the overstory tree canopy also leads to larger raindrops that eventually fall with greater kinetic energy (i.e., throughfall kinetic energy [TKE]) (Geißler et al. 2013). The higher energy of these raindrops can more forcefully affect the adaxial side of coffee leaves, causing vibrations that more easily release mature urediniospores located on the abaxial side of the leaf (Avelino et al. 2020; Boudrot et al. 2016). If, however, winds occur along with rainfall, the negative effect of high TKE appears to be negated, possibly due to the shaking of overstory tree leaves which prevents raindrop accumulation (Boudrot et al. 2016).

Trees interact with wind at the edge of farms by slowing wind speeds via a windbreak effect. This windbreak effect can (i) create a physical barrier to the passive movement of airborne urediniospores (Boudreau 2013; Ratnadass et al. 2012); (ii) reduce wind speeds and turbulence around coffee plants within agroforestry systems, in turn limiting the wind-driven release of *H. vastatrix* urediniospores from sporulating lesions and the distance dispersed urediniospore can travel (Boudreau 2013); and (iii) reduce wind speeds on the leeward side of windbreaks, in turn promoting urediniospore settling from the still air (Pasek 1988). This interaction with wind has implications beyond the individual coffee agroforest, which will be discussed in the following sections.

Agroforestry Management for Coffee Leaf Rust

Tree canopy and leaf traits

Recent advances have been made in relating the effects of canopy characteristics (e.g., height, leaf area index, and canopy architecture) and leaf traits (e.g., specific leaf area, leaf thickness, and leaf angle) in coffee-based agroforestry systems on air temperature, relative

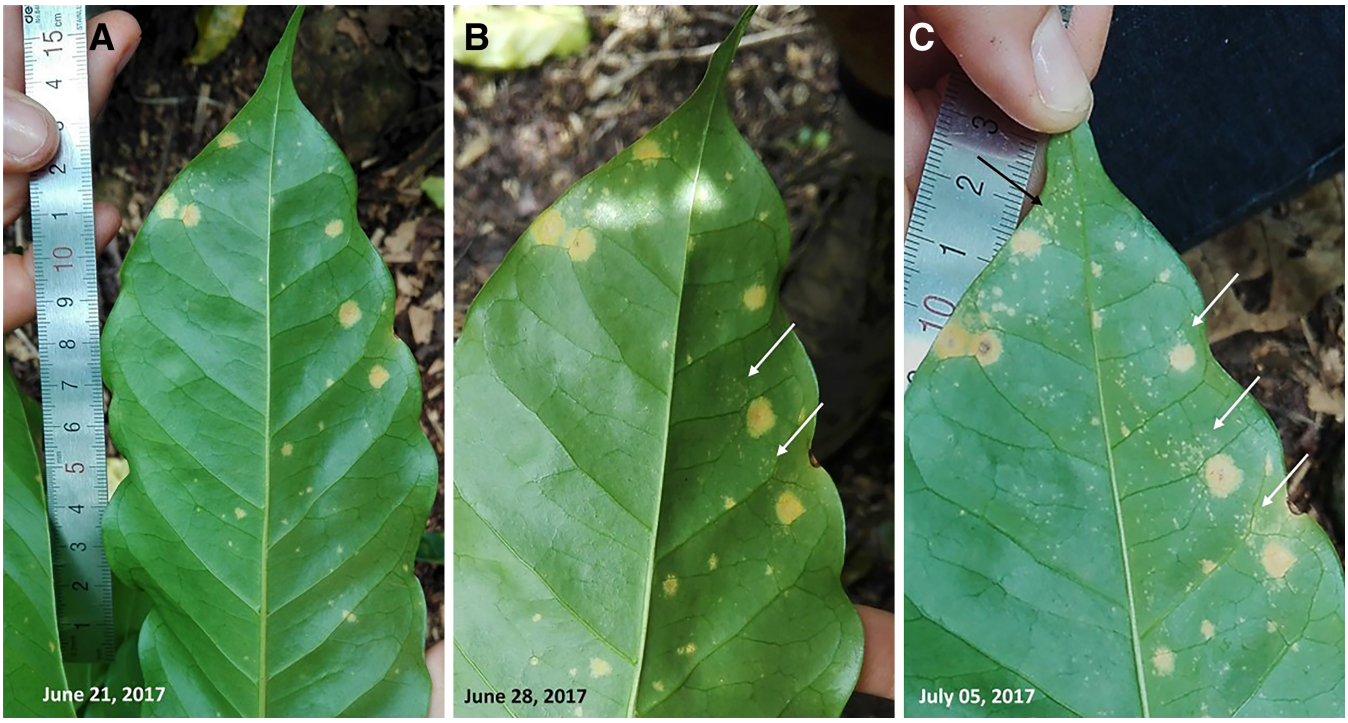

Fig. 7. Spread of *Hemileia vastatrix* urediniospores on a single leaf over time with **B and C,** possible short distance dispersal patterns (arrows) from **A and B,** older initial lesions. Photographs courtesy of Steven Cerdas.

humidity, leaf temperature and wetness, and wind dynamics (Gagliardi et al. 2020, 2021; Merle et al. 2022). To understand the role of tree traits in the moderation of coffee leaf rust life cycle stages, further exploration pairing tree traits and critical abiotic pathways linked to coffee leaf rust disease patterns is key.

As previously discussed, trees can modify raindrop size, kinetic energy, and throughfall amount via rainfall interception and redistribution. However, this ability largely depends on the tree's canopy and leaf traits. For instance, stemflow, which can decrease the amount of rain arriving on coffee leaves, is maximal in tree canopies that are large in area and volume, with more steeply angled branches (wide angle to the ground) and water-repellant leaves (Iida et al. 2005; Martinez-Meza and Whitford 1996) (Fig. 8A). In contrast, throughfall is maximal in tree canopies that are thin, open, and with low leaf area index (LAI) (Nanko et al. 2008; Park and Cameron 2008; Siles et al. 2010b) (Fig. 8B). Throughfall amounts are initially lower as the canopy is undergoing wetting (Nanko et al. 2008), temporarily storing raindrops on leaf surfaces, which depends on the amount of leaves in the canopy (i.e., LAI) and individual leaf area (Aston 1979). The storing of raindrops within the canopy, however, also leads to larger raindrops, which results in throughfall with markedly greater kinetic energy (Avelino et al. 2020; Geißler et al. 2013). This variability in TKE is related to individual tree canopy and leaf traits, with consensus that TKE increases with increasing leaf area, canopy base height, and total canopy height (Geißler et al. 2013; Goebes et al. 2015) (Fig. 8C), whereas TKE decreases with increasing canopy thickness and number of branches (Goebes et al. 2015; Nanko et al. 2008) (Fig. 8D). However, TKE has been observed to increase with both increasing (Geißler et al. 2013; Goebes et al. 2015) and decreasing (Liu et al. 2018; Song et al. 2018) LAI, and the location beneath the canopy and the number of tree species present affects the variability in TKE (Geißler et al. 2013; Liu et al. 2018; Song et al. 2018). At the leaf scale, TKE is reduced under simple, dentate evergreen leaves compared with pinnate or entire deciduous leaves (Goebes et al. 2015). Notably, not all tree traits have the same magnitude of effect on TKE (Geißler et al. 2013), and the influence of traits on TKE can vary based on rainfall intensities (Goebes et al. 2015).

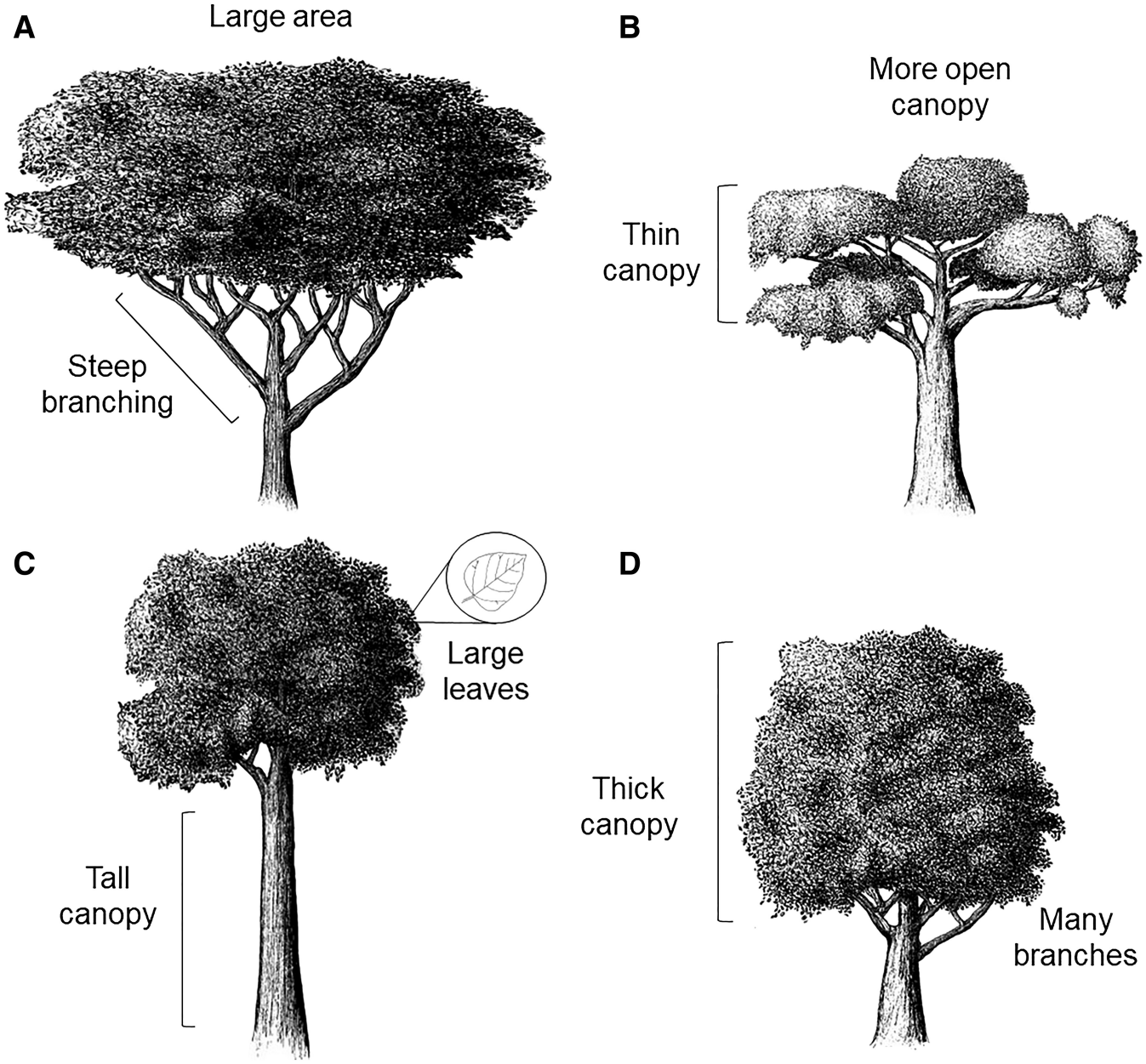

Fig. 8. Desirable tree traits to **A,** increase stemflow; **B,** increase throughfall amounts; **C,** increase throughfall kinetic energy; and **D,** decrease throughfall kinetic energy. Drawing by Stephanie Gagliardi.

Given that wind is an important driver of urediniospore dispersal, we can analyze the windbreak effect of trees from a trait perspective. At the edge of coffee-based agroforestry systems in Costa Rica, dense *E. poeppigiana* trees (mature, large, and unpruned) with thick leaves significantly reduced throughflow wind speed into the farm more than sparse *E. poeppigiana* trees (Gagliardi et al. 2020). However, this reduction in wind speed corresponded to increased airborne urediniospore capture at the coffee plant level at the interior edge of the agroforest, suggesting greater urediniospore settling. This highlighted a potential tradeoff as wind speeds declined (Gagliardi et al. 2020), suggesting either the need for specific tree spatial arrangements (discussed below), or the potential to use other tree traits to enhance the capture and retention of the airborne urediniospores (Cameron and Blanuša 2016). For example, needles of conifers efficiently capture particles from 10 to 100 µm, likely due to the needles' long and thin shape that creates a thin boundary layer that increases the contact probability with airborne particles (Jin et al. 2021). Other leaf surface properties such as roughness with wrinkles, ridges, and furrows; hairy characteristics (trichomes); and the presence of waxes with lipophilic properties on leaves can increase the capture of large airborne particles (>2.5 µm) such as *H. vastatrix* urediniospores compared with smooth, hairless, and glossy leaves (Chiam et al. 2019; Corada et al. 2021; Dzierżanowski et al. 2011). For example, Chiam et al. (2019) showed that trichomes increase the

Table 3. Reported effects of canopy and leaf traits on abiotic pathways (rainfall and wind dynamics)

Traits	Effect on abiotic pathways	Source
Canopy		
↗ Canopy area and volume	↗ Stemflow	Iida et al. 2005; Martinez-Meza and Whitford 1996
↗ Steeply angled branches	↘ Throughfall	
↘ Canopy thickness	↗ Throughfall	Nanko et al. 2008; Park and Cameron 2008; Siles et al. 2010b
↗ Canopy openness		
↘ Leaf area index		
↗ Total canopy height	↗ Throughfall kinetic energy	Geißler et al. 2013; Goebes et al. 2015
↗ Canopy base height		
↗ Canopy thickness	↘ Throughfall kinetic energy	Goebes et al. 2015; Nanko et al. 2008
↗ Number of branches		
↗ Leaf area index	↗ ↘ Throughfall kinetic energy	Geißler et al. 2013; Goebes et al. 2015; Liu et al. 2018; Song et al. 2018
↗ Canopy volume (unpruned trees)	↘ Throughflow wind speed	Gagliardi et al. 2020
Leaf		
↗ Leaf area	↗ Throughfall kinetic energy	Goebes et al. 2015
Pinnate or entire deciduous leaves		
Simple dentated evergreen leaves	↘ Throughfall kinetic energy	Goebes et al. 2015
↗ Leaf thickness	↘ Throughflow wind speed	Gagliardi et al. 2020
↗ Roughness, trichomes and waxes	↗ Capture capacity of particles	Chiam et al. 2019; Dzierżanowski et al. 2011
↘ Specific leaf area (associated with smaller and thicker leaves)		
↗ Roughness	↘ Adherence of particles	Barthlott and Neinhuis 1997

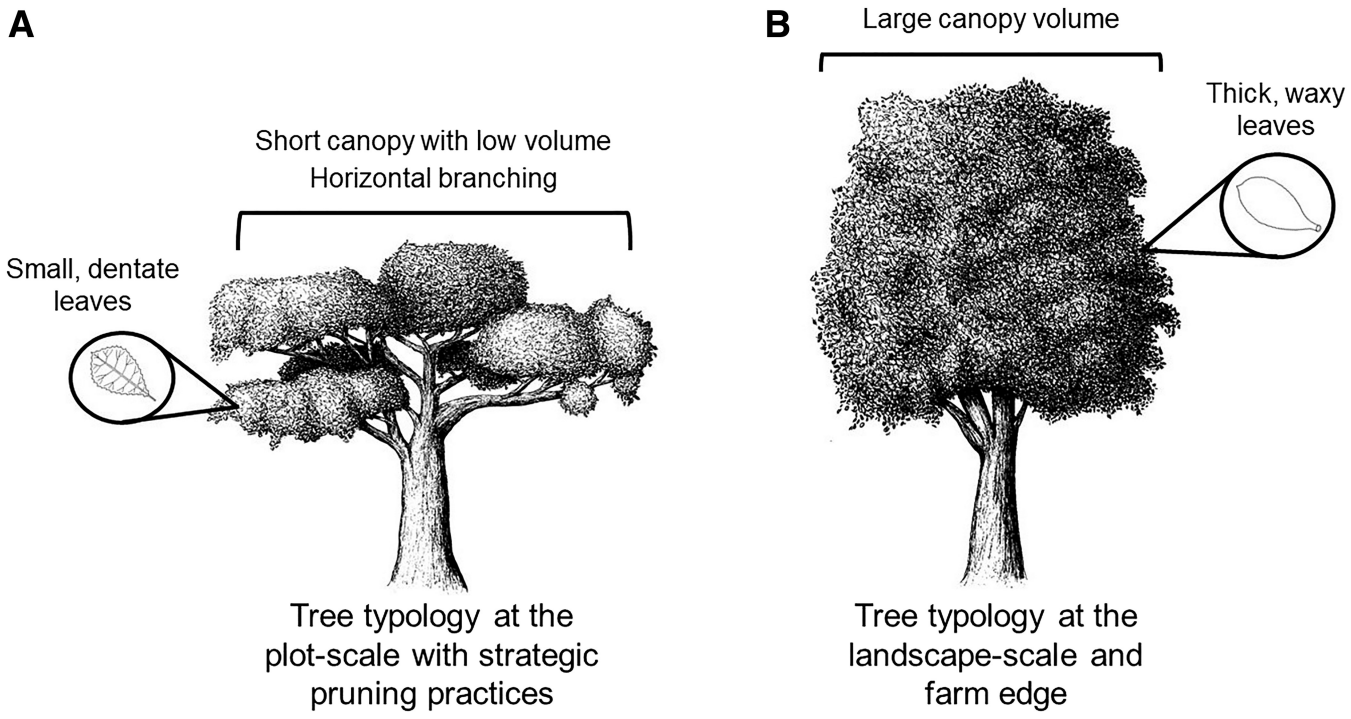

Fig. 9. Tree typologies for coffee leaf rust management at the **A,** plot and **B,** landscape scales. Drawing by Stephanie Gagliardi.

capture capacity of leaves with low specific leaf area (ratio of leaf area to leaf dry mass), a characteristic of smaller, thicker leaves. Though urediniospores can be captured by tree leaves and temporarily retained in the tree canopy, leaves with water-repellent properties (such as rough leaves) prevent water droplets from adhering to their surface, resulting in water droplets and deposited particles rolling off their surfaces (Barthlott and Neinhuis 1997). In contrast, on smooth leaves, water droplets tend to adhere to the leaf surface, resulting in deposited particles being redistributed on the leaf surface.

The influence of specific tree traits on many of the other important abiotic processes related to coffee leaf rust life cycle stages has not been as explicitly outlined compared with those described above. Rather, it is more likely that combinations of tree traits influence microclimate conditions such as air temperature, relative humidity, and leaf wetness duration in combination with macroclimatic conditions. Preliminary studies based in Costa Rica have highlighted the important role of tree canopy height and size and leaf size in affecting various abiotic processes related specifically to coffee leaf rust (Gagliardi et al. 2021; Merle et al. 2022), though this area of research has a lot of potential to grow.

Suggested tree typologies

Based on the consolidated information on tree canopy and leaf traits and their impacts on coffee leaf rust development pathways (Table 3), we propose tree typologies for coffee-based agroforestry systems to assist in managing coffee leaf rust at different spatial scales. It is important to note that these proposed typologies should be used only as a guide, because locally adapted trees with all of the traits we will list likely do not exist in all coffee-growing regions. Rather, the goal should be integrating trees that combine as many favorable characteristics as possible to add to the management of coffee leaf rust. At the plot scale (Fig. 9A), thin canopies with low volume, high openness, and mainly horizontal branching are preferred to increase rain throughfall amount and, in turn, encourage urediniospore wash-off. Notably, a tradeoff between leaf wash-off and higher TKE is important to balance. As such, further preference is given to trees with short canopy base height and small, dentate leaves, which will reduce TKE within the farm. At larger landscape scales, tree typology changes (Fig. 9B), because reducing throughflow wind speed is important to create a barrier to urediniospore travel. As such, large trees of greater canopy volume can decrease throughflow wind speed and trees with small, thick, waxy leaves can increase the capture capacity of airborne particles, thus avoiding the transmission of urediniospores across landscapes.

Tree spatial arrangement and management

In addition to tree traits, the spatial arrangement and management of trees in coffee-based agroforestry systems affect coffee leaf rust dynamics at multiple spatial scales, including the local scale (i.e., coffee plant to coffee plant), farm scale, and larger landscape scale (i.e., between coffee farms).

At the local scale, the greater the density of coffee plants, the more likely plant-to-plant dispersal of *H. vastatrix* will be successful, simply due to the greater probability of physical contact between coffee plants and the shorter dispersal distances required for urediniospores to travel to new hosts. The density of coffee plants within a farm is negatively correlated with the number of shade trees. This is likely due, in part, to the different traditions in agroforestry systems versus unshaded monocultures, and also as a consequence of the shade trees occupying spaces that would otherwise be allotted to coffee plants (Moguel and Toledo 1999). Theoretical work has also shown that the interaction of the spatial patterning of coffee plants within a farm and the local scale dispersal of *H. vastatrix* are central in structuring coffee leaf rust dynamics (Hajian-Forooshani and Vandermeer 2021). In particular, regular lattice-like planting geometries are more susceptible to coffee leaf rust epidemics with relatively small changes in pathogen dispersal distances, compared with irregular planting geometries. Though irregular planting patterns may be due to a lack of deliberate planning during plantation establishment (Gidoin et al. 2014), avoiding lattice-like geometries can be integrated into the planning phase of coffee-based agroforestry systems in order to enhance the management of coffee leaf rust in the long term.

As summarized in Table 2, trees can have undesirable effects on coffee leaf rust at the farm scale; however, these undesirable effects can be moderated via specific management practices and spatial arrangements. For example, to restrict TKE and, therefore, the potential short-distance dispersal of mature urediniospores to new host tissue, vertical canopy stratification can be enhanced and overstory tree canopies can be kept unpruned to maximize canopy thickness and the number of branches (Goebes et al. 2015; Nanko et al. 2008) (Fig. 8D). In contrast, to promote throughfall amounts reaching the understory and, therefore, the potential to wash off urediniospores from mature lesions (Avelino et al. 2020), overstory tree canopies can be pruned to be thinner and more open (Nanko et al. 2008; Park and Cameron 2008; Siles et al. 2010b) (Fig. 8B). With these examples we see the important role that overstory tree pruning can play in throughfall dynamics (Niether et al. 2018) and, therefore, coffee leaf rust dynamics. Pruning recommendations are further complicated by the interaction of tree pruning on multiple microclimate conditions simultaneously (e.g., air temperature moderation and light transmittance) (Niether et al. 2018), and the temporal and spatial variability in macroclimatic conditions (e.g., recommending pruning in wetter conditions when rain is the main driver of urediniospore dispersal, and avoiding pruning in drier conditions when wind is the main driver of dispersal) (López-Bravo et al. 2012).

With respect to the horizontal distribution of shade cover, lessons learned from the pathogen *Moniliophthora roreri* in cacao agroforestry systems (Gidoin et al. 2014), which has some similarities with *H. vastatrix*, indicate that uniform distribution of shade cover (i.e., avoiding large gaps in the canopy) is preferable. This way, no highly favorable conditions for any stage of the disease will be found within the farm.

The spatial arrangement of trees can be further manipulated to enhance the beneficial impacts of trees at the farm scale, such as their windbreak effect. As described above, Gagliardi et al. (2020) captured more airborne urediniospores at the coffee plant level at the internal edge of coffee agroforests, likely due to the slower wind speeds at that position promoting urediniospore settling. With such observations, trees can be arranged to create a buffer zone surrounding agroforestry systems, where urediniospores can prematurely settle out of the incoming air currents, effectively removing them from the infection cycle and preventing their further travel into the coffee farm.

Regarding the landscape scale, the windbreak effect of trees both around farms and in the general landscape (Fig. 10) are also desirable to disrupt urediniospore transport by wind to connected coffee farms (Hajian-Forooshani and Vandermeer 2021; Vandermeer and Rohani

Fig. 10. Coffee landscape in Costa Rica with **A,** coffee-banana agroforestry system; **B,** unshaded coffee monoculture; and **C,** unshaded coffee monoculture with windbreaks along perimeters. Photograph courtesy of Jacques Avelino.

2014; Vandermeer et al. 2015). For instance, Avelino et al. (2012) related increased local epidemics of coffee leaf rust with landscapes dominated by low-wind-resistance land uses (i.e., open pasture), because these landscapes likely favored greater wind turbulence and the release of urediniospore clusters compared with landscapes with greater wind resistance (i.e., treed areas). From a more general theoretical level, there are two pools of dispersed urediniospores: (i) in the general atmosphere traveling long distances and (ii) within a coffee farm moving among coffee plants. Therefore, considering both processes, the greater the density of urediniospores on a farm, the greater the farm's contribution to the urediniospore load in the atmosphere, and the greater the urediniospore load in the atmosphere, the greater potential deposition of urediniospores into the farm. Although these nonlinear dynamic processes can produce a sudden outbreak of the disease, formally called a critical transition (Vandermeer and Rohani 2014), the presence of trees within agroforestry systems and within the broader landscape reduces the likelihood of that occurring (Vandermeer et al. 2015).

Research Perspectives and Conclusions

Based on detailed knowledge of the factors driving coffee disease development and the interacting and complex effects of trees in agroforestry systems, we and others have shown that it is possible to identify key tree traits, spatial arrangements, and management practices that can make the integration of trees into disease management practices more effective.

There are very few studies trying to understand the relationships between tree traits and management of diseases in agroforestry systems. One of the first studies was published by Gagliardi et al. (2020) on the relationships between tree traits at the edge of coffee farms, wind interception, and *H. vastatrix* dispersal. Such an approach should be developed for other life cycle processes, at other scales, and in a variety of spatial contexts, to verify that the promising hypotheses mentioned in the previous sections can indeed help manage coffee leaf rust. In these analyses, it is vital that the relative contribution of each process or subprocess to epidemic development be determined, so that the key tree traits needed to effectively impede epidemic development can be distinguished.

The combination of process-based epidemiology, modeling, and functional trait ecology is also useful for other relevant plant diseases. Due to the complex and dynamic microclimatic requirements of diseases, it is vital to study all regulation pathways potentially complicated by trees in agroforestry systems, because tradeoffs in tree traits and management are likely inevitable. This higher level of complexity can be more easily addressed by modeling approaches that quantitatively integrate tree traits and management options, with supplemental field experiments. This research is important to determine the usefulness of trees in agroforestry systems in aiding disease management practices, in addition to the many other ecosystem services that trees can provide.

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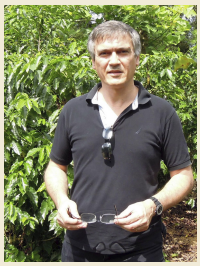

Jacques Avelino

Jacques Avelino is a plant pathologist in the Plant Health Institute of Montpellier (France) at CIRAD (French Agricultural Research Center for International Development). He holds a Ph.D. from the University of Orsay (Paris XI). His research program focuses on the effects of trees on coffee pests and diseases, in particular the coffee leaf rust caused by *Hemileia vastatrix* on which he has been working since 1986. He has also developed research on frosty pod rot of cacao caused by *Moniliophthora roreri*. During his career, he has conducted research and development projects in Central America, mainly in Costa Rica with CATIE (Center for Tropical Agricultural Research and Education), Mexico, the Caribbean, Venezuela, Laos, Indonesia, and Papua New Guinea.

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Stephanie Gagliardi is an agroforestry specialist with PUR Projet, where she supports the design, implementation, and monitoring of smallholder agroforestry systems around the world. She recently completed her Ph.D. from the Department of Physical and Environmental Sciences at the University of Toronto. Her research aimed to advance integrated disease management strategies by investigating the dynamic links between ecosystem processes and multi-species trait interactions in agroforestry systems. Her work continues to explore plant-soil interactions, pest and disease dynamics, and overall ecosystem functioning in agroforestry systems to help inform sustainable farm design and management practices.

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Ivette Perfecto is the James E. Crowfoot Professor of Environmental Justice at the School for Environment and Sustainability of the University of Michigan. She has more than 35 years of experience working on issues of agriculture and the environment. Her research focuses on agroecology, biodiversity, and ecosystem services in agricultural landscapes with an emphasis on agroforestry systems of Mexico and Puerto Rico. She has more than 200 publications in peer-reviewed journals and is author with John Vandermeer of four books: *Breakfast of Biodiversity* (2005), *Nature's Matrix: Linking Agriculture, Conservation and Food Sovereignty* (also with Angus Wright; 2009 and 2019), *Coffee Agroecology* (2015), and *Ecological Complexity and Agroecology* (2017). Professor Perfecto was one of the lead coordinating authors of the United Nation's International Assessment on Agricultural Knowledge, Science and Technology for Development (IAASTD). She has received several awards including the ESA Diversity Award, SNRE Outstanding Teaching Award, and University of Michigan Faculty Recognition Award. She is an elected senior fellow of the American Association for the Advancement of Science (AAAS), senior fellow of the Ecological Society of America (ESA), and a senior fellow of the Michigan Society of Fellows. Professor Perfecto was elected to the U.S. National Academy of Sciences in 2022. She has been a member of the New World Agriculture and Ecology Group and Science for the People for more than 30 years.

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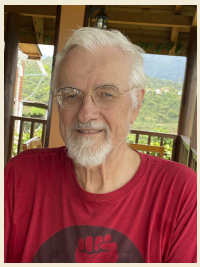
Theresa Liebig is a systems analyst with more than 10 years of experience in tropical agroecological and smallholder systems in Central America and East Africa. Her research on coffee-based agroforestry systems has focused on coffee pest and disease abundance and ecological mechanisms in Arabica coffee production systems in the face of climate change. She is currently an associate scientist at the CGIAR FOCUS Climate Security Research, which aims to understand how climate can act as a threat multiplier for conflict and insecurity. She holds an M.Sc. in agricultural biology from the University of Hohenheim and a Ph.D. in horticultural science from the University of Hannover.



John Vandermeer

John Vandermeer is Asa Gray Distinguished University Professor and Arthur R. Thurnau Professor of Ecology and Evolutionary Biology and a professor in the Program in the Environment at the University of Michigan. He teaches three courses: 1) food, energy, and environmental justice, 2) the ecology of agroecosystems, and 3) complex systems in ecology. His research focuses on the coffee agroecosystem for which he delves into recent advances in complex systems in attempting to understand the biological, social, and political aspects of this important ecosystem. He is author or editor of 16 books and over 250 scientific publications.

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Isabelle Merle is a postdoctoral researcher at the IRD (French national research institute for sustainable development) in the EGCE research unit (Evolution, Génomes, Comportement, Ecologie). Her research involves field trials and ecological modeling to study the effect of microclimate and management practices on diseases, pests, and pollinators in agro-ecosystems such as tropical perennial agroforestry systems. She has mainly conducted studies on coffee and cocoa crops with projects in Central America on coffee leaf rust with CIRAD (French Agricultural Research Center for International Development) and CATIE (Center for Tropical Agricultural Research and Education) and projects on self-incompatibility in cocoa with the MARS Company, INRAE (French national research institute for agriculture, food and the environment), and CATIE. With IRD, she currently investigates the effects of practices on cocoa entomofauna in Colombia, Ecuador, Costa Rica, and Cameroon and cocoa pollinator efficiency.

Zachary Hajian-Forooshani

Zachary Hajian-Forooshani is a Ph.D. student at the University of Michigan in the Department of Ecology and Evolutionary Biology working with John Vandermeer and Ivette Perfecto. He is primarily interested in agroecology, community ecology, and spatial ecology. His research broadly aims to understand how the assembly of novel communities within agroecosystems impact the dynamics of ecological processes and subsequent provisioning of ecosystem services. His dissertation is concerned with the dynamics of coffee leaf rust and its community of natural enemies in Mexico and Puerto Rico.

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Natacha Motisi holds a Ph.D. in epidemiology from Agrocampus Rennes, France. She is now researcher at CIRAD (Centre International en Recherche Agronomique pour le Développement, France) and posted at ICIPE (International Centre of Insect Physiology and Ecology) in Nairobi, Kenya. She has a 12 years' experience in epidemiology of *Coffea arabica* diseases and mechanistic modeling of the dynamics of the diseases at the tree, plot, and territorial scales. Her objective is to define the levers of action, in particular agroecological practices, making it possible to durably reduce the diseases.

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