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Interactive effects of altitude, microclimate and shading system on coffee leaf rust

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ABSTRACT

Shade effects on coffee diseases are ambiguous because they vary depending on the season and environment. Using Coffee Leaf Rust (CLR) as an example, we demonstrate relationships between the environment and shading systems and their effects on disease intensity. We characterized seasonal variations in microclimate and CLR incidence across different altitudes and shading systems, and integrated effects between the environment, shading systems, microclimate and CLR into a piecewise structural equation model. The diurnal temperature range was higher in unshaded systems, but differences decreased with altitude. Humidity related indicators in shaded systems decreased with altitude. At mid and high altitudes, high CLR incidence occurred in the shading system showing a low diurnal temperature range and a high dew point temperature. Our study demonstrates how microclimatic indicators vary as a function of the season, altitude and the coffee shading system, and how this in turn is related to CLR.

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Hemileia vastatrix; coffee; shade; microclimate; piecewise structural equation modelling

Introduction

Coffee agroecosystems are interaction networks consisting of anthropogenic, topographic, meteorological, edaphic and biological components, which vary in space and time (Wagenet 1998). The performance of the coffee system with respect to different ecosystem services is a function of complex space and time-dependent interactions, which can emerge as trade-offs or synergies (Cerda et al. 2016). Sustainable pest and disease management strategies require an understanding of the complexity of agroecosystems (Avelino et al. 2006; Cerda et al. 2016).

The performance of coffee, e.g. productivity (Vaast et al. 2006), quality (Bosselmann et al. 2009), biodiversity (Teodoro et al. 2010) or sustainability (Jha et al. 2011) under shaded vs. sun-exposed conditions has been explored in numerous studies. Beneficial shading effects on coffee production through the mitigation of microclimatic extremes have been quantified and are generally well-established (Barradas and Fanjul 1986; Lin 2007). It has also been acknowledged that the extent to which shaded systems are advantageous depends on the biophysical context (Cerda et al. 2017; Rahn et al. 2018).

Since shading effects vary across sites and season, its impacts on coffee pests and diseases are ambiguous (Avelino et al. 2006, 2011; López-Bravo et al. 2012; Boudrot et al. 2016). Few studies were conducted across different temporal and spatial scales or focused on the effect of multiple factors and response variables. With the availability of both spatial data and statistical tools to evaluate networks of causal relationships (Grace 2006; Lefcheck 2016), recent research addresses the complexity of agroecosystems (Boreux et al. 2013; Allinne et al. 2016).

Shading modifies the environment for pests and diseases directly or indirectly via changes in microclimate, or by creating habitats for beneficial or competitive organisms (Avelino et al. 2004; Pumariño et al. 2015). Likewise, shade modifies the environment for many other components of the system, e.g. coffee physiology and productivity, soil, water, as well as biodiversity, which in turn may also be related amongst themselves and with pests and diseases (Muschler 2004). Moreover, these ecological mechanisms of shade are altered by greater spatial factors, such as macroclimatic variations along altitudinal or latitudinal gradients (Staver et al. 2001; Avelino et al. 2011; Cerda et al. 2017).

The case of Coffee Leaf Rust (CLR, *Hemileia vastatrix*) illustrates how shade can operate in two antithetic pathways: shade may (i) aggravate the disease due to modifying the microclimate to conditions more favorable for the fungus or (ii) regulate yield, which in turn could negatively affect the pathogen because attack intensities are more acute when fruit load is high (Avelino et al. 2004, 2006; López-Bravo et al. 2012).

CLR has caused tremendous damage for the Arabica coffee sector of the Americas over the past few years (Avelino et al. 2015). The combination of suboptimal management and meteorological factors were responsible for the heavy outbreaks and this is expected to play a role under future climate conditions (Avelino et al. 2015). In Africa, CLR is the most devastating disease of Arabica coffee after Coffee Berry Disease (*Colletotrichum kahawae*) (Matovu et al. 2013). In

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Uganda, the impact of CLR became apparent in the 1940s when areas of land typically producing Arabica, had to be replaced with Robusta coffee (McCook 2006).

In this study, we explore direct, indirect and interactive effects of the altitude and coffee shading system on microclimatic indicators and CLR. We (i) characterized seasonal variations in microclimate and CLR incidence across different altitudes and shading systems. We then (ii) integrated effects between the environment, shading systems, microclimate and CLR into a conceptual and statistical framework to understand directional relationships.

Material and methods

Study area

The study was conducted in three districts that produce Arabica coffee in the Mt Elgon area of eastern Uganda (Figure 1). The area, dominated by smallholder agriculture, has an altitude of 1000–2200 masl. We sampled three altitude ranges (see S1, Supporting Information), low (1100–1400 masl), mid (1400–1700 masl) and high (1700–2200 masl). The area has a bimodal rainfall with peaks in March/April and October/November and is dry in December–February. Annual rainfall is 1200–1800 mm, with mean temperature from 18 to 23°C, depending on altitude. Smallholders grow coffee with varying shade-tree species and density, with bananas or with no shade. Traditional, CLR susceptible varieties such as SL 14, SL 28 and Nyasaland are grown (Matovu et al. 2013).

Plot selection and characterization

We selected sites based on a survey conducted in 2014 (Rahn et al. 2018). In summary, along the three altitude ranges we created typologies of shading systems using descriptors of the vegetation structure. Table 1 shows which shade-related descriptors we used and how we characterized them (see also S1, Supporting Information). Based on those typologies, a total of 49 plots (0.03–0.5 ha) were used for the present study.

Data acquisition

On each plot, we systematically selected nine coffee bushes on a cross-shaped transect representing the shading system of the whole plot. We avoided exhausted, too old (>30 years) or too young (<five years) bushes and those on plot borders to avoid boundary effects. On each coffee bush, six branches in the lower, mid and higher vegetation storey (two per storey) and facing towards different directions were marked. CLR was assessed on these branches by counting healthy and diseased leaves (identified by chlorotic or yellow spots on the lower leaf surface) in approximately six-week intervals from the beginning (March) until the end (December) of 2015 growing season. We installed the temperature and relative humidity data loggers (iButton® DS1923) on a subset of 27 plots (three replicates for each system by three altitudes). We installed two screened loggers (Holden et al. 2013) on each plot at the height of 1.50 m, and set them to record each hour during the 2015/2016 season.

Table 1. Characteristics of production typologies generated by K-means clustering.

	CO		CB		CT	
	n = 54		*n* = 44		*n* = 46	
	Mean	SE	Mean	SE	Mean	SE
Coffee density (coffee ha^{-1})	2255^{a}	125	2094^{a}	127	2095^{a}	112
Banana density (bananas ha^{-1})	29^{a}	17	1496^{b}	105	278^{c}	82
Shade tree density (trees ha^{-1})	63^{a}	6	49^{a}	6	146^{b}	16
Shade tree species richness	2.8^{a}	0.2	2.7^{a}	0.2	6^{b}	0.4
Canopy Closure (%)*	21^{a}	1.4	28^{b}	1.4	48^{c}	2

*Canopy closure indicates the average plot shade estimated using a spherical crown densiometer (Forestry Suppliers, convex model A) (Lemmon 1957) at four random positions within the plot. SE = Standard error. Means within rows with different letters indicate significant differences (one-way ANOVA, $p < .05$). Clustering was based on a total of 144 plots, which were sampled in May 2014. In 2015, 22 additional plots were included and classified retrospectively. CB = Coffee-Banana System, CO = Coffee-Open System, CT = Coffee-Tree System. These plots were used for coffee leaf rust assessments.

Explanatory and response variables

Explanatory variables included the altitude range (representing a set of topographical indicators), and coffee shading system. Microclimatic variables served as both, response variables as a function of the altitude range and coffee shading system, as well as explanatory variables for CLR. Microclimatic variables explaining CLR variability were generated and selected in two steps. First, we did a literature review to identify microclimatic variables driving CLR epidemics (Table 2 and S2 of the supporting information). Identified variables (or a related variable if the measurement was not

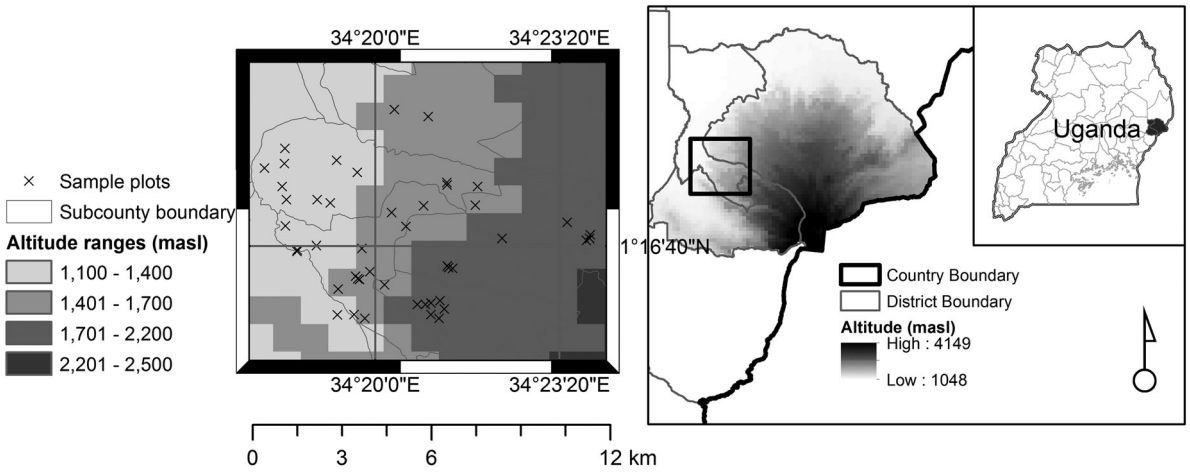

Figure 1. Study area within the Ugandan Mount Elgon area and the districts (Bulambuli, Kapchorwa and Sironko).

Table 2. Literature review[a] on microclimatic variables driving coffee leaf rust epidemics.

Microclimatic drivers of CLR	Reference	Description	Derived variables selection procedure[b]
Temperature (mean, maximum or minimum)	(Rayner 1961; Nutman et al. 1963; De Jong et al. 1987)	Bimodal relation between temperature and CLR spore germination/appressorium formation (optimum range between 21°C and 25°C). Optimum temperature for lesion formation at 22°C. De Jong et al. (1987) reported a broader range (16–28°C) for germination and appressorium formation, the latter being stimulated by low temperatures	(1) Mean daily, (2) mean nightly[c], (3) maximum, (4) minimum temperature,
Diurnal temperature range (DTR)	(López-Bravo et al. 2012; Avelino et al. 2015)	Lower diurnal temperature range favors CLR infection and reduces the latent period of infection	(1) Diurnal temperature range (DTR)
Light	(Rayner 1961; Bock 1962; Nutman et al. 1963)	Light has a retarding but not inhibiting effect on spore germination. Germination is favored by darkness (e.g. at night), but can also occur during the day in dependence of rainfall and temperature.	-
Humidity (RH) and rainfall	(Rayner 1961; Bock 1962; Nutman et al. 1963; Kushalappa 1982)	The presence and duration of liquid water is essential for CLR germination and infection. Rainfall plays a role in wetting the undersurface of coffee leaves and in spore dispersal	(1) Relative humidity (RH) (2) Dew point (DP) (3) Number of hours with temperatures below DP at night[c,d] (4) Number of hours with RH above 95% at night[c,d]
Leaf wetness	(Avelino et al. 2004; López-Bravo et al. 2012)	Higher leaf wetness frequency/duration favors CLR intensity	

[a]Based on Avelino et al. (2004).
[b]For each monitoring date, the mean of the 4-weeks interval (counting backwards from the monitoring date) was extracted. Given a latent period of approximately three weeks (Leguizamón 1983) and incubation period of four to seven weeks (Rayner 1961), the four-week interval was considered as reasonable.
[c]In East Africa, infection processes occur between 10 pm and 8 am (Rayner 1961), therefore some variables representing the night time hours were extracted.
[d]Based on an empirical model (Rowlandson et al. 2015), leaf wetness duration is equal to the number of hours in which the RH (measured 1.5–2.0 m above the ground) is equal or greater than 90%.

available) were derived from our microclimate recordings, totalling nine microclimatic variables. Second, to select time periods for each variable, four-week time intervals for each monitoring date were extracted. The final number of potential CLR driving microclimatic variables totalled 63 (9 variables × 7 monitoring dates). The maximum CLR incidence (CLR_{max}) of the season, i.e. the number of diseased leaves as a proportion of the total number of young leaves (according to Avelino et al. 1991, determined by the short internode resulting from the dry season) per bush was the response variable. Explanatory and response variables are summarized in Table 3.

Data analysis

(i) Characterization of seasonal variations of microclimate and CLR

We identified microclimatic variables and corresponding 4-week time intervals by plotting them against CLR_{max}. We excluded highly autocorrelated predictors by estimating the correlation coefficients matrix.

The CLR_{max} and the selected microclimatic variables were plotted per altitude range and coffee shading system to illustrate seasonal variations. Differences among the altitude and shading system gradients were tested with the method described in the following paragraph.

(ii) Formulation of a piecewise structural equation model (SEM)

Based on literature and field observations, we developed an *a priori* conceptual model of the possible underlying relationships between components of the environment, coffee shading system, microclimate, coffee productivity and coffee pests and diseases (Figure 2). Table 4 shows which variables were considered and how they were used in the subsequent analysis.

We used a piecewise structural equation model (SEM) to infer direct and indirect effects of altitude and coffee shading system on CLR_{max} via microclimatic indicators. An SEM is a statistical framework used to understand causalities within complex natural systems (Shipley 2000; Grace 2006). The hypothetical causal relationships are represented in a graphical model, where each path describes directional relationships between variables. We used piecewise SEM enabling generalized linear models to be fit to different distributions, including those typical for pest and disease data. Individual paths are estimated separately and then combined to a series of equations to estimate direct and indirect effects within the system (Lefcheck 2016).

The piecewise SEM was constructed based on the conceptual model in Figure 2 and the results of the selection procedure of potential microclimatic variables. First, each response variable, i.e. the microclimatic variables and CLR, representing the component models or paths, were fitted as linear or generalized linear models in dependence on individual or combined predictors. For each path, the best model was selected by Akaike information criterion (AIC). Then, the individual models were combined to a list of equations and applied to the piecewise SEM function. Non-significant paths ($p > .05$) were excluded from the overall model. The Shipley's test of d-separation was used to test whether significant paths were missing. The Fisher's C statistic evaluated the overall fit of the model.

We used R software (R Core Team, 2016) with RStudio (Version 0.99.903) for data analysis. We used ArcMap (ESRI, 2014) to produce the maps. We used the 90-m resolution digital elevation model of the shuttle radar topography mission and the administrative borders from the Data.Ug database (http://maps.data.ug/).

Table 3. Recorded, explanatory and response variables used in the structural equation model.

	Initial available/ recorded variables	Retained explanatory/response variables		Description
Topoclimate[a]	Altitude (masl) Slope (°) Slope aspect (°)	Explanatory	Altitude class (Alt.)	Key variables of climate and topography were subjected to a cluster analysis. The determinant variable was altitude, with the remaining variables being correlated. Low < 1400 masl Mid = 1400–1700 masl High > 1700–2200 masl
Vegetation structure	No. of shade trees/ha No. of shade tree species No. of banana mats/ha Canopy closure (%)	Explanatory	Typology of coffee shading system (CS)	Clustering of the vegetation structure of coffee plots resulted in three different coffee shading systems classified as CB = Coffee-banana system CO = Coffee open canopy system CT = Coffee-tree system whereas the CO system shows the lowest, and the CT system highest shade levels (Table 1).
Microclimate	Temperature (°C) Relative humidity (%)	Explanatory/ Response	Non-correlated microclimatic indicators[b]	
Disease indicator	CLR incidence	Response	Maximum CLR incidence (%) (CLR_{max})[c]	The maximum disease incidence (mean per plot) of the season (CLR_{max}). Monitoring dates: (1) March/April, (2) May/June, (3) July/August, (4) September, (5) October/November (6) January (7) February

[a]Topographic variables (altitude, slope and slope aspect) of the study area were generated from a digital elevation model (90 m DEM) of the shuttle radar topography mission.
[b]Microclimatic indicators resulting from the selection procedure described in the subsequent data analysis section.
[c]The maximum incidence of the season was reported to be a good indicator of epidemic intensity (Kushalappa and Chaves 1980; Silva-Acuña and Zambolim 1999; Avelino et al. 2006).

Results

(i) Characterization of seasonal variations of microclimate and CLR

Microclimatic variables and time periods related to CLR_{max} are shown in Table 4. Results of the selection process are shown in detail in S3a-b of the supporting information.

Figure 3 shows the seasonal patterns of selected microclimatic indicators grouped by altitude range and coffee system. The mean night time temperature (TempN) differed between the three coffee systems in the period between May and September. It was lowest in coffee-tree (CT) at low, in coffee-banana (CB) at mid, and in coffee open canopy (CO) at high altitudes. The diurnal temperature range (DTR) was higher in CO systems in all altitudes, but less pronounced in the low altitude range. The dew point temperature (DP) at low altitude was constantly lower in CO systems over the season. At mid-altitude, the mean DP over the season was lower in CT systems, while differences were marginal at high altitudes. The number of night hours with relative humidity >95% (RH95) in CO systems was lowest at low

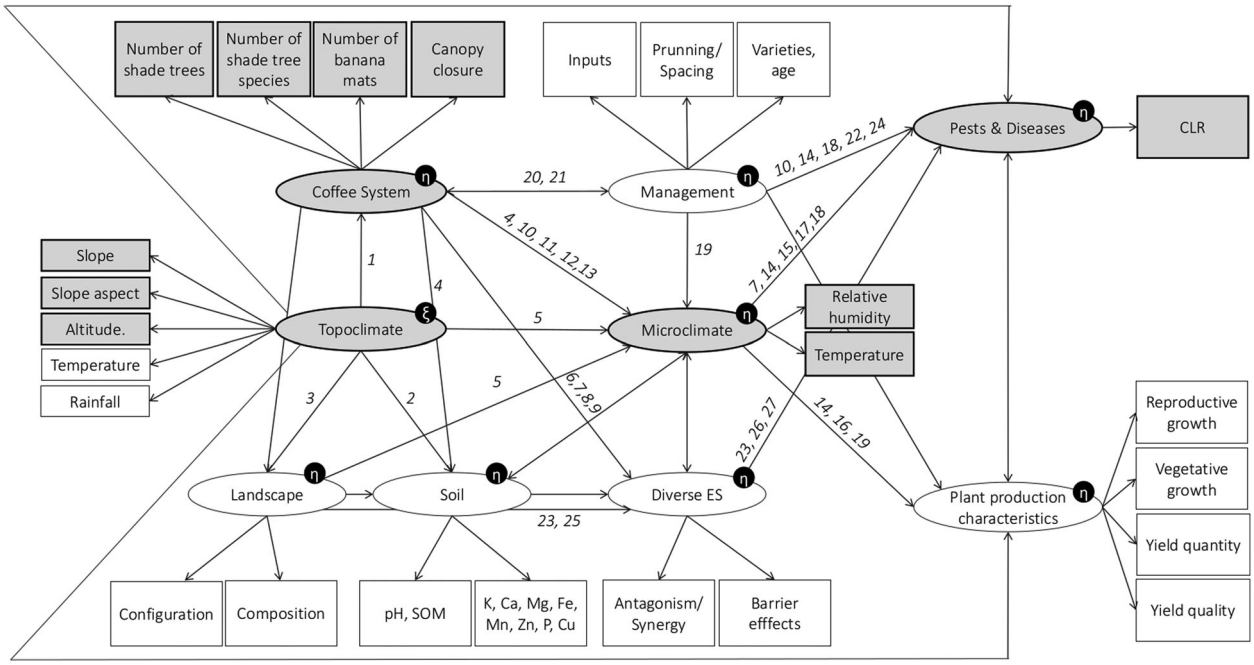

Figure 2. A priori conceptual model (based on literature review, Supporting Information, S2) of the possible underlying relationships between components of the environment, coffee shading system, microclimatic indicators, coffee productivity and coffee pests and diseases. Ovals represent latent constructs (unobserved variables), and boxes manifest (observed) variables. Endogenous constructs (dependent variables) are indicated by η, and exogenous (independent variables) by ξ. Numbers 1–27 refer to literature references. Arrows indicate the directional relationships between latent constructs, representing individual paths to be modeled in the piecewise SEM approach. Grey shaded fields show the variables used in the subsequent piecewise SEM. The indicated sub-system shows the relation between topoclimate and coffee system, both characterized by a set of observed variables, modifying the environment for coffee pests and diseases either directly and/or indirectly via microclimate.

Table 4. Selected microclimatic variables.

Selected microclimatic variables[a]	Selected time periods[b]
Night temperature (TempN)[c]	July–September[d]
Dew point temperature (DP)[e]	May–November
Number of night hours with RH > 95% (RH95)[c]	September–November
Diurnal temperature range (DTR)[e]	September–November

[a]Variable selection based on literature review (Table 2).
[b]Remaining variables and time periods excluding highly correlated predictors.
[c]Means per night.
[d]Time periods within a variable of microclimate were autocorrelated and hence were combined to one variable for the piecewise structural equation model (e.g. dew point temperature of the four time periods were used as the mean dew point temperature for the period between May–November).
[e]Means per day (24 h).

altitude and highest at high altitudes, while at mid altitudes it was highest in CB systems.

Figure 4 shows the CLR disease process of the 2015/2016 growing season as a sigmoid-shaped growing curve typical for a polycyclic epidemic. At low and mid altitudes, symptoms appeared approximately two months after the rainy season (June/July), when newly grown leaves were fully developed. An exponential increase in CLR incidence followed across the short dry spell around August/September and the second rain flush in October/November, peaking in the main dry season during December until February. The amount of disease at low and mid altitudes was similarly high, while the incidence was lower at high altitudes, where CLR developed after the second rainy season. The CLR incidence in the different systems did not differ at low altitudes. At mid and high altitudes there was a downward gradient of disease incidence from CB to CO and CT systems.

(ii) Formulation of piecewise structural equation model (SEM)

The piecewise SEM was fitted to infer the effects of the selected microclimatic variables, the altitude class, and coffee system on the maximum CLR incidence. Each component model corresponding to the five response variables, i.e. the four selected microclimatic variables (Table 4) and CLR_{max}, represented one path. Two DP (May–Nov.), DTR (Sept.–Oct.) of the four response functions for the microclimatic variables were significant paths ($p < .05$). The list of component models consisted of three equations:

$$CLR_{max} \sim Alt\_cat \times CS + DP\_{MN} + DTR\_{SO}, \quad (1)$$

$$DP\_{MN} \sim Alt\_cat \times CS, \quad (2)$$

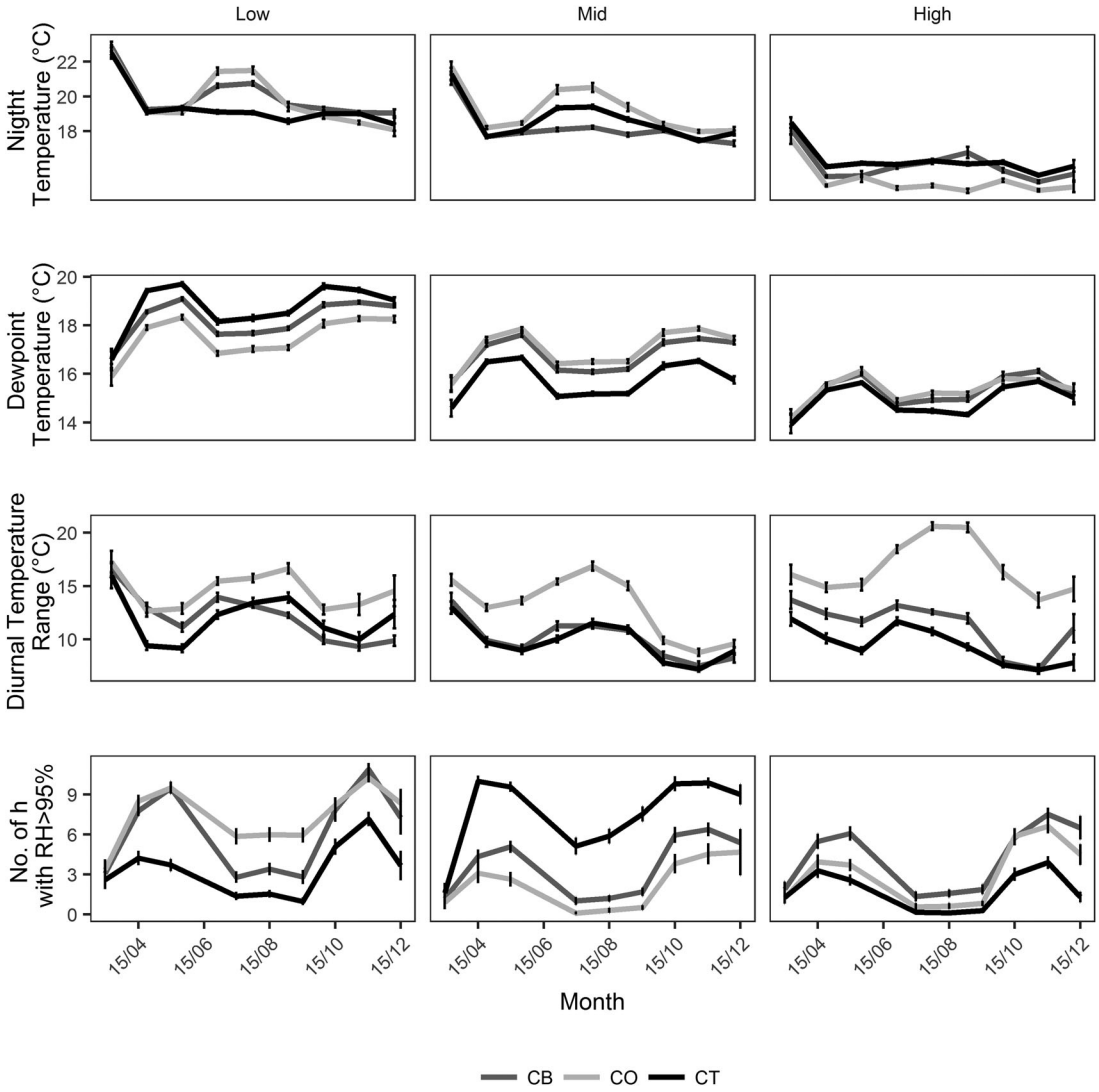

Figure 3. Microclimatic indicators over the 2015/2016 growing season. Variables represent monthly means with standard errors. CB = Coffee-banana system, CO = Coffee open canopy system, CT = Coffee-tree system. Altitude ranges were low (1100–1400 masl), mid (1400–1700 masl) and high (1700–2200 masl). Loggers with missing data were excluded.

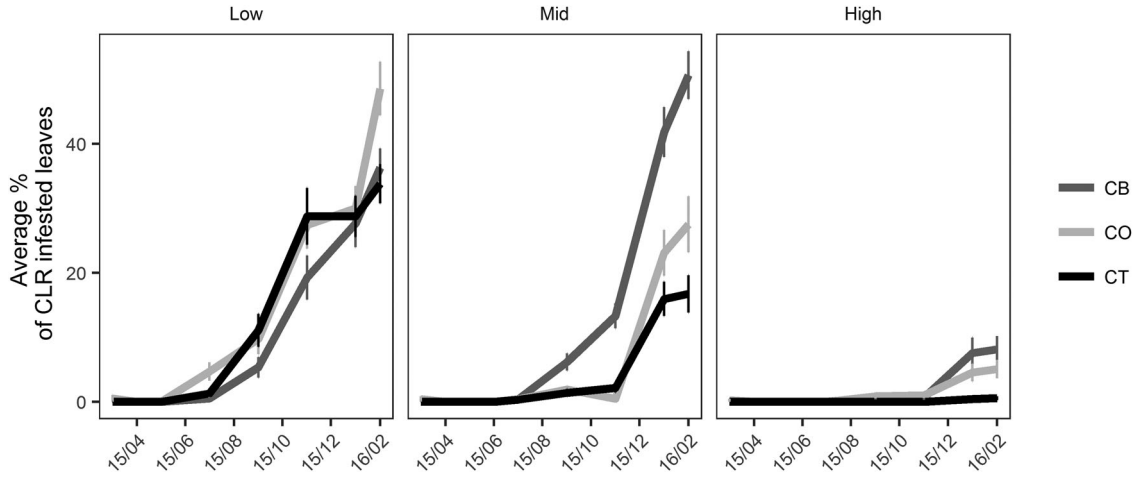

Figure 4. CLR disease process curves of the 2015/2016 growing season. The curves represent the average CLR incidence per monitoring date ($n = 49$), grouped by altitude range and coffee shading system. CB = Coffee-banana system, CO = Coffee open canopy system, CT = Coffee-Tree system. Altitude ranges were low (1100–1400 masl), mid (1400–1700 masl) and high (1700–2200 masl).

$$DTR\_{SO} \sim Alt\_cat + CS, \quad (3)$$

where CLR_{max} is the maximum disease incidence, Alt_cat the altitude category, CS the coffee shading system, DP_{MN} the average dew point temperature of May–Nov and DTR_{SO} the average diurnal temperature range of Sept–Oct. CLR_{max} was fitted as a generalized linear model with a negative binomial distribution, with DP_{MN} and DTR_{SO} as linear models.

The piecewise SEM ($p > .05$, Fisher's C, AIC = 59.01) showed interactive, direct and indirect effects of the altitude classes and coffee systems on CLR_{max} (Figure 5). CLR_{max} was predicted to be lower in CT systems, ($\beta = -3.00156$, $p < .0001$), but was also determined by an interacting effect of altitude and system. Highest CLR_{max} were predicted in CO systems at low altitude, but in CB systems at mid and high altitudes. The average DP (May–Nov.) was higher at low and mid, compared to high altitudes ($\beta = 3.1892$, $p < .0001$, $\beta = 1.4821$, $p < .0001$, respectively) and there was a combined effect of altitudes and systems with lowest values in CO systems at low, and in CT systems at mid altitudes ($\beta = 0.6929$, $p < .05$ and $\beta = -0.6220$, $p < .05$). The DTR was highest in CO systems ($\beta = 3.4354$, $p < .0001$) and lowest at mid altitudes ($\beta = -1.5199$, $p < .05$). The Model showed indirect effects of altitude and coffee systems on CLR_{max}, mediated by the microclimatic variables. DTR was negatively ($\beta = -0.2731$, $p < .0001$) and DP positively ($\beta = 1.5577$, $p < .001$) related to CLR_{max}.

Discussion

We have shown that the effects of the environment (altitude) and coffee shading system (shading) on CLR variability are either direct, interactive or indirectly mediated by key microclimatic indicators. Our case study on CLR illustrates an approach also applicable to other (patho)- systems to describe interactions in agroecosystems.

Literature on microclimatic drivers shows that among others, CLR development is dependent on variables related to the presence of liquid water and temperature (De Jong et al. 1987; Avelino et al. 2004; López-Bravo et al. 2012). The microclimatic indicators we identified as CLR drivers (dew point temperature (DP) and the number of hours with RH > 95% (RH95)), relate to dew formation. We also found temperature related variables, especially the DTR, to be decisive for CLR. A lower mean DTR results in shorter latency periods because the temperature is closer to its optimum for infection processes (Waller 1982; Avelino et al. 2012; López-Bravo et al. 2012). Night temperatures also affect CLR epidemics. Since germination is favored by darkness (Bock 1962; Nutman et al. 1963), most infections occur at night (Rayner 1961).

It is well established which main factors drive CLR epidemics. However, few studies have investigated how those

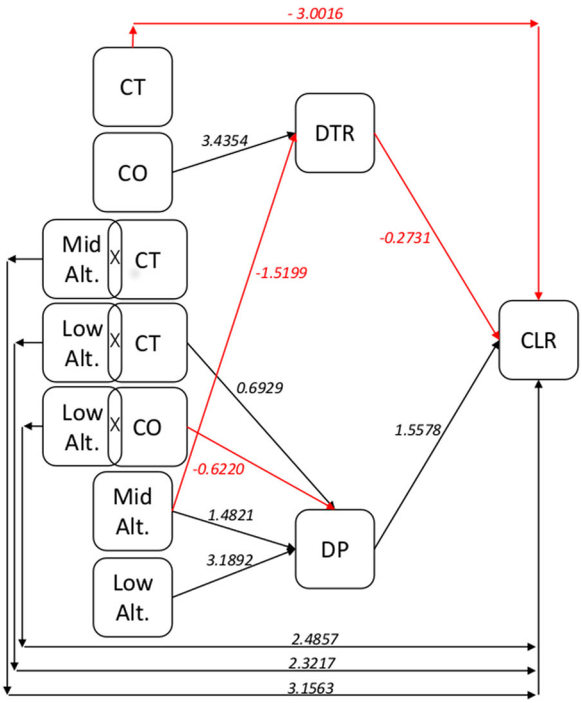

Figure 5. Final path model selected through the piecewise SEM procedure. Solid black arrows show positive, solid red arrows negative paths. The standardized coefficient for each path from the individual models are illustrated. Reference categories (data not shown) for the coffee shading system and altitude range are CB and high altitude. Crosses indicate an interacting effect of two categories. Shipley's test of d-separation was used to estimate the overall fit of the model (chi-squared test on the Fisher's C statistic results in $P > .05$ if no paths are missing). CT = Coffee-Tree system, CO = Coffee-Open system, Alt. = Altitude range; low (1100–1400 masl), mid (1400–1700 masl), DTR_SO = Diurnal Temperature Range (September-October 2015), DP_MN = Average Dew Point temperature (May–November 2015), CLR_max = the maximum disease incidence.

microclimatic drivers themselves vary in space and time and how this in turn would be related to CLR. We showed that microclimatic indicators varied as a function of the season, altitude and the coffee shading system. At higher altitudes, humidity indicators decreased in the systems with highest shade (CT) compared to the lowest shade density and diversity (CB and CO). This contradicts the widely-accepted notion of higher moisture and leaf wetness in shaded versus non-shaded systems (Barradas and Fanjul 1986; Beer et al. 1998; Morais et al. 2006). The consistently highest DTR values of CO systems agreed with reports of existing literature (Barradas and Fanjul 1986; Lin 2007). However, while differences at low altitudes were negligible, they strongly increased with altitude.

The variability of microclimatic variables across altitudinal gradients, shading systems and seasons can be explained by processes of surface energy fluxes (Shuttleworth 2012). Dew formation is driven by the interplay between air moisture, temperature variations and cooling of plant surfaces via radiation (Xiao et al. 2013). This in turn is influenced by cloudiness, wind speed, soil water content and water vapor pressure and hence by altitude and vegetation cover (Linacre 1982; Dai et al. 1999). Diurnal fluctuations are extreme at high altitudes and under sun-exposed conditions. The reduced atmospheric pressure causes higher maximum and lower minimum temperatures due to rapid insolation and reduced radiation (Linacre 1982; Mani 2013). Clouds as well as shade tree cover buffer these effects, which on the one hand results in a lower DTR in shaded systems (Dai et al. 1999), but also reduced night-time radiation (Morais et al. 2006) and hence less dew formation. In contrast, reduced minimum or night temperatures in unshaded systems increase the nocturnal soil emissivity and hence, dew formation. Those dynamics are furthermore altered by the seasons. Changes in solar radiation, precipitation and cloudiness imply a seasonality in surface energy fluxes and hence microclimate (Dai et al. 1999; Xiao et al. 2013). Our data also show these seasonal effects. DTR was lowest and DP/RH95 was highest during the rainy seasons (Apr./May and Oct./Nov.), when cloud cover was high.

Differences in microclimatic conditions driven by the environmental and seasonal context influence CLR dynamics. At mid altitudes, highest CLR incidence was found in CB systems, where DTR was low and DP high (Avelino et al. 2015). The same reasoning applies for high altitudes, although disease incidence was low due to low mean temperatures. At low altitudes, differences between systems in both microclimatic variability and CLR incidence were minor. Our results agree with the findings of other studies, where CLR was reduced at high altitudes in highly diversified systems (Avelino et al. 2006; Cerda et al. 2016). CLR development was also related to the seasonal changes of microclimate. The microclimate differed between altitude ranges and systems during the rainy seasons. In the first season, this may be less important because leaves that are not fully developed are resistant to infection (Eskes 1982). In addition, fruit loads, positively related to CLR severity (Avelino et al. 2006) are low during this time. Leaf susceptibility grows with fruit growth (Kushalappa and Chaves 1980), therefore microclimatic conditions during the second rainy season might be decisive. In coffee-growing regions with a pronounced dry season such as in our study area, the residual inoculum is minimized by the shedding of diseased leaves and lack of new infections (Bock 1962). However, in areas without a clear dry season, microclimatic conditions might influence the inter-seasonal survival of rust spores and disease built-up in the subsequent season (Waller 1982).

The mediated effects of the environment and coffee shading system through the local microclimate on CLR are fundamental. They co-occur, however, as shown in our conceptual model (Figure 2), with a diversity of other influencing factors. Though not addressed in the present study, they are conceptually incorporated within the piecewiseSEM. The altitude range and the shading system are latent constructs; therefore, their direct and interacting effects must be mediated through further mechanisms and variables one way or the other.

Our results validate approaches of other studies that showed how production situations (the ecological, technical, social, economic context of agricultural systems (Rabbinge and De Wit 1989)) and crop management are linked to crop health and that they can be considered as proxies for microclimate (Avelino et al. 2004; Savary et al. 2017). This is not only important for pests and diseases in coffee-based, but also other tropical agroecosystems that form heterogeneous mosaics of small thermal microhabitats (Potter et al. 2013). The impact of micro-environments on crop health are understudied and their ecological relevance understated (Stigter 2015). This is especially relevant in the context of adaptation to climate change.

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