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Abstract

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In complex coffee-based agroforestry systems, quantifying the impact of shade trees on coffee disease regulation and coffee yield is crucial for improving these systems and designing more sustainable ones. To this end, we analyzed interactions amongst shade trees, coffee plants (cv. Catimor), the coffee foliar disease complex and soil characteristics. We studied systems characterized by 40 variables measured in 60 plots located on three farms (monitored for 2 years) in Nicaragua. These variables characterized six system components grouped in six statistical blocks: shade trees (shade percentage and species abundancy), soil characteristics (fertility), foliar diseases, coffee plant characteristics (age and size), coffee growth and yield. We used partial least square path modelling (PLS-PM), i.e. a structural equation modelling approach used to understand and quantify interactions between the six blocks. Shade trees (mostly the associated shade percentage) had direct positive effects on foliar disease severity and incidence and soil quality, while having negative effects on coffee growth and yield. Soil characteristics (carbon, nitrogen, litter index, water infiltration potential) were negatively correlated with foliar diseases. An excessive shade percentage then had an indirect negative effect on coffee growth and yield due to the increased prevalence of foliar diseases. Finding the optimal shade cover can help reduce foliar diseases and enhance coffee berry production. The 'dose effect' of shade cover must also be considered because excessive shade, as well as lack of shade, have negative impacts on coffee growth and yield. Overall, effective shade management requires an analysis of trade-offs between soil quality, disease regulation and yield gains. In conclusion, PLS-PM turned out to be a good tool for studying agroecosystem networks and enabled us to put forward some foliar disease management and coffee yield enhancement guidelines.

Keywords

Central America; *Coffea arabica*; disease regulation; ecological processes; trade-off; tree-shade impact; structural equation modelling; plant diversity

1. INTRODUCTION

Pests and diseases reduce coffee yields in Central American coffee-based agroforestry systems by 15-30% (Cerda et al., 2015). Sustainable management of these diseases based on agroecological processes, e.g. biological regulation optimization, is thus a key lever to increase coffee yield while maintaining the environmental sustainability of the cropping system. Trees associated with coffee plots support biological regulation to a major extent through direct and indirect processes (Ratnadass et al. 2012). Direct regulation effects that reduce diseases involve different processes, including: 1) dilution of host density, 2) reduction of soil diseases by favoring beneficial microorganisms, 3) allelopathic effects, 4) reservoir of natural enemies, and 5) creation of microclimates unfavourable for the diseases (Ratnadass et al. 2012). Shade trees may have indirect beneficial effects on coffee plants, mostly by enhancing coffee nutrition (Sauvadet et al. 2018). In complex agroecosystems with high spatially heterogeneous plant diversity associated with coffee plants, unravelling the direct and indirect effects of shade trees on all coffee crop systems is a great challenge.

Nicaragua is eighth largest *C. arabica* producing country in the world, with production reaching 2.54 million kg in the 2017-2018 cycle. Coffee cropping has a huge socioeconomic impact in this country, where 44 thousand coffee producers cultivate a total area of 1.5 million ha. Most of the farms grow coffee under agroforestry systems, and 97% of them are less than 14 ha. Nicaraguan coffee-based agroforestry systems are known to be particularly complex with a remarkable diversity of shade trees (Haggar et al., 2015). This diversity includes species that produce goods for local markets, native forest species that are grown mainly for timber, along with service tree species — mostly Fabaceae — that are planted to provide shade while improving soil fertility and crop system sustainability (Barradas and Fanjul, 1986; Vaast et al., 2005). The coffee rust outbreak that occurred in 2013–2014 led farmers to replace the rust-sensitive cv. Caturra plants in their coffee plantations with rust-resistant cv. Catimor plants (Libert Amico et al., 2019). However, Catimor cultivars are particularly sensitive to the American leaf spot (ALS) disease caused by *Mycena citricolor* (Sequeira 1958; Staver et al., 2001; Allinne et al., 2016). Other diseases like brown-eye spot (*Cercospora coffeicola* Berk. & Cooke*)*, anthracnose (*Colletotrichum* sp.) and coffee thread blight (*Corticium kolegora*) also affect cv. Catimor coffee plants (Waller et al., 2007). These foliar diseases have negative effects on coffee growth and production, and interact with each other as a disease complex depending on the coffee crop status and the microclimatic conditions. A major way to improve disease management is to integrate the role of shade trees on these foliar diseases (Avelino et al., 2018; Allinne et al., 2019). Indeed, ALS and coffee thread blight are favored by high humidity when shade levels are elevated, unlike brown-eye spot and anthracnose that tend to affect sun-grown coffee plants (Staver et al., 2001; Muller et al., 2008; Bedimo et al., 2012). Most Nicaraguan farmers do not have sufficient financial resources to manage pests and diseases using pesticides (Bro et al., 2019). Understanding the relations within disease complexes that affect coffee plants and the diversity of shade trees is crucial and requires an overview of the entire pathosystem.

In these complex agroforestry systems, shade trees do not just provide shade to the crop system, they also have directly impact coffee growth and yield by increasing the leaf surface and coffee quality (Vaast et al., 2005; Charbonnier et al., 2017). Conversely, shade trees and coffee plants can compete for light and nutrients, especially under high shade tree density conditions (Charbonnier et al., 2013). However, shade trees may also markedly alter the soil characteristics, and in some cases improve soil fertility (Sauvadet et al., 2018). This is well-known by farmers who often plant nitrogen-fixing trees (e.g. *Inga* spp.) to favor nitrogen fixation (Cerdán et al., 2012). These interactions between shade trees and agroecosystem processes are also driven by farmers through their pruning practices whereby the canopy is opened and dead branches are left on the ground (Cerdán et al., 2012). This litter addition around coffee plants may enhance soil fertility and promote the activity of beneficial soil microorganisms (Sauvadet et al., 2018). Coffee plant resistance against foliar diseases is dependent on these soil characteristics. Indeed, coffee plants growing in more fertile soil have higher regeneration properties and growth, which are key physiological resistance factors (Ratnadass et al., 2012). Soil fertility also influences the quality and abundance of coffee beans produced (Barel and Jacquet, 1994; Lin, 2010).

New tools are needed to study this network of interactions between different agroecosystem components overall. We used a structural equation modelling (SEM) approach called partial least square path modelling (PLS-PM) to gain further insight into the direct and indirect effects of shade trees on coffee foliar diseases and coffee yield in Nicaraguan coffee-based agroforestry systems.

2. MATERIAL AND METHODS

4.2. STUDY SITES

The study took place in the Matagalpa region (Nicaragua's main coffee production area) near the village of El Tuma–La Dalia. We studied three small coffee farms from May 2016 to February 2018 under conventional, low-input and organic disease management conditions. The farms were chosen for their high shade tree diversity, with marked variability in the proportion of shade, i.e. 49-85% (Table 1). These farms only grew non-certified *Coffea arabica* (Rubiaceae) cv. Catimor plants. This genetic material was rust resistant (no evidence of rust affection was observed during the experiment) but sensitive to American leaf spot caused by *Mycena citricolor* (Allinne et al., 2016; Libert Amico et al, 2019). The farms were located between 13°02'67.7''N and 13°08'75.6''N and between 85°61'42.7''W and 85°71'48.3''W, within a similar elevation range (650-850 m a.s.l.). The mean annual temperature was 23°C, with annual precipitation ranging from 2,000 to 2,600 mm. The rainy season in this region is between May and December (Amores Contreras, 2015).

Table 1. Description of the three farms where the study was conducted in the area around El Tuma-La Dalia, Nicaragua.

	Farm

	Variables	*Unit*	1	2	3
Farm description	Community		Yale 3	Hilipo 2	Aguas Amarillas
	GPS location	*(N, W)*	13.08756, -85.61427	13.03735,-8571483	13.02677,-85.67999
	Elevation	*(m)*	750-800	850	650 - 700
	Area	*(ha)*	5	3	3
Meteorological data	Average temperature [min-max]	(°C)	22.3 [19.2-29]	21.9 [19.2-28.4]	23.9 [21.1-28.7]
	Cumulative rainfull	(mm)	2600	2341	2132
Coffee plot description	Average coffee age	*(year)*	9	6	6
	Coffee density	*(plants/ha)*	8882	8620	8679
	Average shade cover [min-max]	*(%)*	72 [62-77]	65 [49-76]	80 [71-85]
	Average shade tree density	*(tree/ha)*	360	350	487
	Average shade species richness		30	18	37
Coffee crop managment	Weeds	/	manual (3 x)	manual (3x)	chemical: glyphosate+ paraquat
	Diseases	/	copper (Bordeaux mixture) (1x)	copper (Bordeaux mixture) (1x)	carbendazim (2x)
	Pests	/	/	/	cipermetrina
	Fertilization	/	/	biofertilizer (foliar)	NPK (20-5-20)

4.3. AGROFORESTRY SYSTEM CHARACTERIZATION

For each farm, we selected 20 circular plots (14 m dia.), centered on a shade tree and sorted in four different situations, with five replicates each. The first three situations were based around three common tree species spread on the farms, while the last situation was made around a random tree, from another tree species. The common species were: 1) *Cordia alliodora* (Ruiz & Pav.) Oken, laurel (Boraginaceae) a native forest species; 2) *Inga oerstediana* Benth, guaba roja (Leguminosae) service plant species; 3) *Musa* spp. Jussieu, guineo (Musaceae).

The distance between each plot was maximized. Inside each plot, the analysis included: (1) four coffee plants selected randomly within 5 m of the central tree, and (2) all shade trees taller than the coffee plants.

4.3.1. Shade tree characterization

All shade trees within the sampled area were identified according to their species and family. Their characteristics (height (m), circumference (cm), leaf size) and their host status for ALS, brown-eye spot and anthracnose were recorded (Boshier et al., 2009; Cerdán et al., 2012). For all species, we also specified their main usage, and classified them in one or more categories: wood, timber, fruit, shade, N-fixation, native and wild (Pineda, 2006; Boshier et al., 2009; Román et al., 2012; Amores Contreras, 2015; Caceido, 2016).

We combined the variables describing each shade tree by performing a multiple factor analysis (MFA) to cluster the shade-tree species within homogeneous groups based on the previously described variables. MFA was performed with R software using the MFA function from the FactoMineR package (Pagès, 2013).

We took hemispherical pictures to characterize the shade percentage at four different times: November 2016, February 2017, June 2017 and September 2017. Hemispherical pictures were taken above all selected coffee plants with a Nikon Coolpix 4500 equipped with a fisheye converter (FC-E8 0.21x). These pictures were analyzed using Gap Light Analyzer (GPA-V2) software to assess the shade percentage above each coffee tree (Frazer et al., 1999). The annual mean shade percentage was used for the analysis.

4.3.2. Coffee tree characterization

The coffee plant variables were measured from May 2017 to February 2018, describing:

- Inherent coffee characteristics not affected by the local environment, such as age (years) and circumference (cm).
- Coffee vegetative growth, described by the total number of nodes per branch, the number of new nodes per branch, the number of leaves per branch and the average leaf area. We measured these variables on three branches (one at the bottom, one in

the middle and one at the top of each selected coffee tree). All measurements were obtained at four times, representing a complete annual coffee physiological development cycle: beginning of the rainy season (May 2017), beginning of the harvest period (September 2017), peak of the harvest (December 2017) and post-harvest (February 2018). All physiological variables were integrated over a time course by determining the area under the disease progress curve (AUDPC), as is frequently done for diseases (Simko and Piepho, 2011).

- Coffee yield was described by the number of fruiting branches per plant and the number of fruiting nodes per plant as proxies of the accessible yield. The number of dead branches per coffee plant after harvest is a proxy of primary yield loss (Cerda et al., 2017).

4.3.3. Coffee foliar disease characterization

The measured foliar disease complex encompassed American leaf spot (ALS; *Mycena citricolor)*, brown-eye spot (*Cercospora caffeicola* Berk. & Cooke*)*, anthracnose (*Colletotrichum* sp.) and coffee thread blight (*Corticium kolegora*). We measured the severity (i.e. the percentage of diseased leaves) and the incidence (i.e. the percentage of leaf area affected by diseases) of these diseases on three branches of selected coffee plants. As ALS is a major foliar disease, we decided to treat it separately from other diseases to gain clear insight into the relationship between the agrosystem and the ALS incidence and severity. We separately integrated ALS variation patterns and those of other diseases by calculating the relative AUDPC based on the measurements obtained at four dates (May 2017, September 2017, December 2017, February 2018), which represented a complete disease development cycle.

4.3.4. Soil characterization

Measurements for characterizing the soil in each coffee plot were obtained at the beginning of the 2017 rainy season (between June and August). According to the protocol described by Thoumazeau et al. (2019a, 2019b) and adapted by Andreotti (2018). The measured soil characteristics included:

- The soil chemical composition: organic carbon (g/kg), pH, nitrogen percentage (N), iron (Fe), potassium (K), magnesium (Mg), and phosphorus (P) in ppm. Soil organic carbon and nitrogen are key soil components and are both indicators of soil fertility.
- The litter index accounted for the litter quantity and quality, which highly influences soil fertility, the nutrient cycle while being the main carbon source for soil organisms (Sauvadet et al., 2016).
- The Beerkan test was applied to measure the soil infiltration potential and generate information on the water infiltration potential (Lassabatere et al., 2006).
- The cation exchange capacity (CEC), which expresses the capacity of a soil to retain nutrients, was used as a soil fertility indicator (Chapman, 1965).

All three farms had the same soil physical characteristics, including a loamy sandy texture.

4.4. Statistical analysis

Structural equation modelling (SEM) is particularly appropriate for gainign insight into interactions between shade trees, soil, diseases and coffee plants. SEM analyses are able to explain relationships between observed variables by clustering them as latent variables representative of common concepts. Structural equation modelling analyses can be used to understand complex systems (Hoyle, 2012; Vinzi and Trinchera, 2013) and was successfully applied to analyse ecological regulations in agroforestry systems in banana and cocoa plantation settings (Poeydebat et al. 2017; Oliveira et al., 2018). This type of analysis is divided into two main types: the SEM-ML method based on the maximum likelihood (ML) and the partial least square path modelling (PLS-PM) method based on simple regressions to explain the latent variables (Vinzi and Trinchera, 2013). The PLS-PM method was specifically chosen for its flexibility to manipulate datasets with numerous variables, and its capacity to represent clearly complex interaction systems.

PLS-PM is a blend of two models: a measurement model and a structural model (Fig. 1). The measurement model defines the relationships between observed variables and latent variables inside blocks, with each block being represented by a latent variable and built with observed variables (Fig. 1). The structural model investigates relationships between latent variables using a linear regression approach. We performed this network analysis with R software using the plspm function from the plspm package (Sanchez et al., 2013).

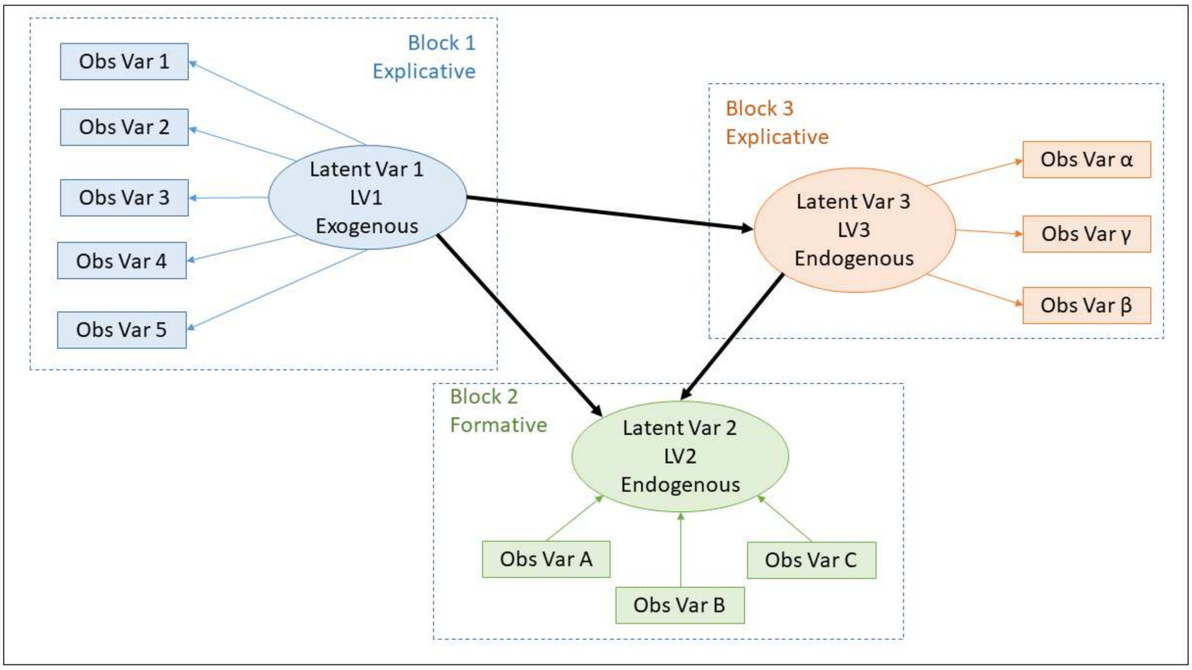

Figure 1. Scheme of the PLS-PM. Description of the measurement model (inside each block) and the structural model (black arrows between blocks). Exogenous latent variables are just explanatory, while endogenous are explanatory and explained (by other latent variable, either exogenous or endogenous). Block 1 and 3 are explicative, while block 2 is formative.

4.5. MEASUREMENT MODEL BUILDING

Our measurement model contained six blocks including latent variables corresponding to the measurement domains presented earlier, i.e. inherent coffee characteristics (hereafter simply called ‘coffee characteristics‘), shade trees, soil characteristics, foliar diseases, coffee growth and coffee yield (Table 2). We built three blocks related to coffee plants because we assumed that these blocks represent a specific aspect of coffee plants, and influence each other. Each block was composed of a latent variable and its related observed variables (Table 2). According to the method described by Sanchez (2013), the coffee characteristics, shade trees, soil characteristics, foliar diseases and coffee growth blocks were reflective because the variables observed inside each block were well correlated. Indeed, for each reflective block, observed variables have to move in the same direction, and when a variable increases or decreases, the others change in the same way (Sanchez, 2013). We verified this condition by examining the unidimensionality of these blocks with Dillon-Goldstein’s rho. A block is unidimensional when its rho value is higher than 0.7 (Sanchez, 2013).

Inversely, the coffee yield block was formative because the numbers of fruiting nodes and fruiting branches were not closely correlated with the number of dead branches. As formative blocks do not require highly correlated observed variables, the block unidimensionality is not calculated.

Table 2. Description of blocks represented by their latent variable and observed variables. ALS is American leaf spot of coffee; organic C is soil organic carbon; N is the nitrogen percentage; iron (Fe), potassium (K), magnesium (Mg), and phosphorus (P) are in ppm; CEC is the cation exchange capacity.

Latent variable	**Related observed variables**
Coffee characteristics	Age, size (circumference)
Shade trees	Shade (%), abundance of services trees, fruit trees and timber trees
Soil characteristics	Litter index, Beerkan test, organic C, N, pH, Mg, Fe, K, CEC
Diseases	ALS severity, ALS incidence, other disease severity, other disease incidence
Coffee growth	Number of nodes, number of new nodes, number of leaves, leaf size, coffee height
Coffee yield	Number of fruiting branches, number of fruiting nodes, number of dead branches

We only kept observed variables that were correlated with the latent variable with a regression coefficient higher than 0.5 (Sanchez, 2013). Inside each block, the regression coefficient value explained how the observed variables influenced the latent variable. Higher coefficients indicated a higher influence on the block.

4.6. STRUCTURAL MODEL BUILDING

The relationship between blocks was defined in the structural model according to previous studies (Fig. 2) (Allinne et al., 2016; Cerda et al., 2017). The latent variables shade trees and coffee characteristics were not explained by the other blocks and threfore were exogenous, while the latent variables soil, diseases, coffee growth and coffee yield were endogenous, because they were explained by the other blocks (Fig. 2).

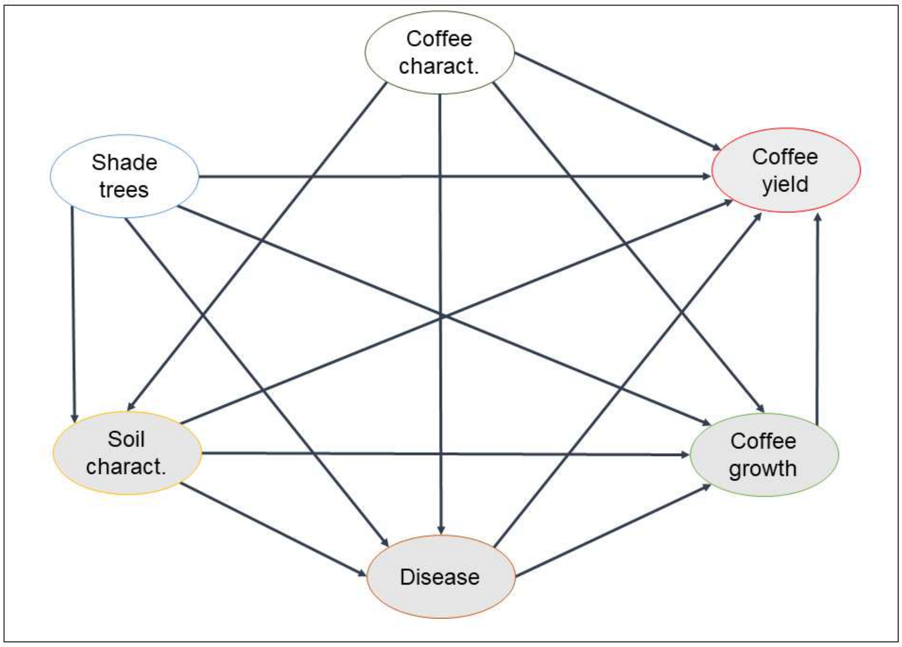

Figure 2. Pathways between the latent variables. Coffee characteristics and shade trees are exogenous (i.e. only explanatory) (white), while soil characteristics, diseases, coffee growth and coffee yield are endogenous (grey).

In order to validate our block, the PLS-PM model was used to calculate the R^2 coefficient of each exogenous block that expressed the explained variability for each block. Other latent variables better explained the block when the R^2 coefficients were high. The model parameters were thus adjusted to have R^2 coefficients higher than 0.2, which is a moderately low value (Sanchez, 2013).

The regression coefficient between blocks clarified the relationship between the block, i.e. either positive or negative.

Finally, the goodness-of-fit test was used to evaluate the model robustness (Sanchez, 2013).

All statistical analyses were performed with the R 3.5.1 package (Team R Core, 2018) and with an alpha level of 0.05.

3. RESULTS

4.1. CLUSTERING OF SHADE TREES

The MFA led to three groups of shade tree, i.e. timber, service and fruit trees. The timber group was composed mostly of native and forest species intended for wood production. The service group had shade-tree species, mostly N-fixing species, that were planted to improve the soil quality and shade percentage, though some of these species were hosts of some coffee foliar diseases like ALS. The fruit group was represented mostly by species producing secondary fruit products sold in local markets or consumed locally. These groups were used in the PLS-PM model to build the 'shade trees' block.

4.2. PLS-PM MODEL OUTPUT

The measurement model and structural model results shed light on the complex network of interactions between shade trees, coffee plants, foliar diseases and soil characteristics. While the measurement model showed the block compositions, the structural model revealed the strength of the relation between them. The overall PLS-PM had a goodness-of-fit of 0.4971.

4.3. RELATIONSHIPS BETWEEN THE OBSERVED AND ASSOCIATED LATENT VARIABLES (WITHIN BLOCK)

The measurement model findings showed that all reflective blocks (‘coffee characteristics’, ‘shade trees’, ‘soil characteristics’, ‘diseases’ and ‘coffee growth’) had a Dillon-Goldstein’s rho higher than 0.7 (Fig. 3). The correlation coefficients between the observed and associated latent variables were higher than 0.5, except for the ‘other-disease severity’ variable in the diseases block (Fig. 3). Although the ‘other-disease severity’ variable had a coefficient of 0.41, we decided to keep it in the model because it provided a better representation of the pest complex in the system (Fig. 3).

The ‘coffee characteristics’ latent variable was well-explained by its two observed variables, i.e. age (0.96) and circumference (0.91) (Fig. 3). From the ‘shade trees’ block, only the observed variables of the mean shade percentage (M. shade, 0.94) and service group (Serv, 0.64) had a significant impact. The ‘soil characteristics’ latent variable was explained only by the Beerkan test (0.83), organic carbon quantity (0.6) and nitrogen percentage (0.62), as well as the litter index (0.68). The ‘soil characteristics’ parameter thus represented the soil fertility. The ‘diseases’ block was mainly explained by the observed variables related to ALS severity (0.94) and ALS incidence (0.94). The remaining observed variables that explained the ‘coffee growth’ block were the height (0.6), number of nodes (0.87), number of new nodes (0.9) and number of leaves (0.55). Inside the ‘coffee yield’ block, the number of fruiting branches per tree was more significant (0.87), it was correlated with the number of fruiting nodes (0.76) per branch and with the number of dead branches (0.56).

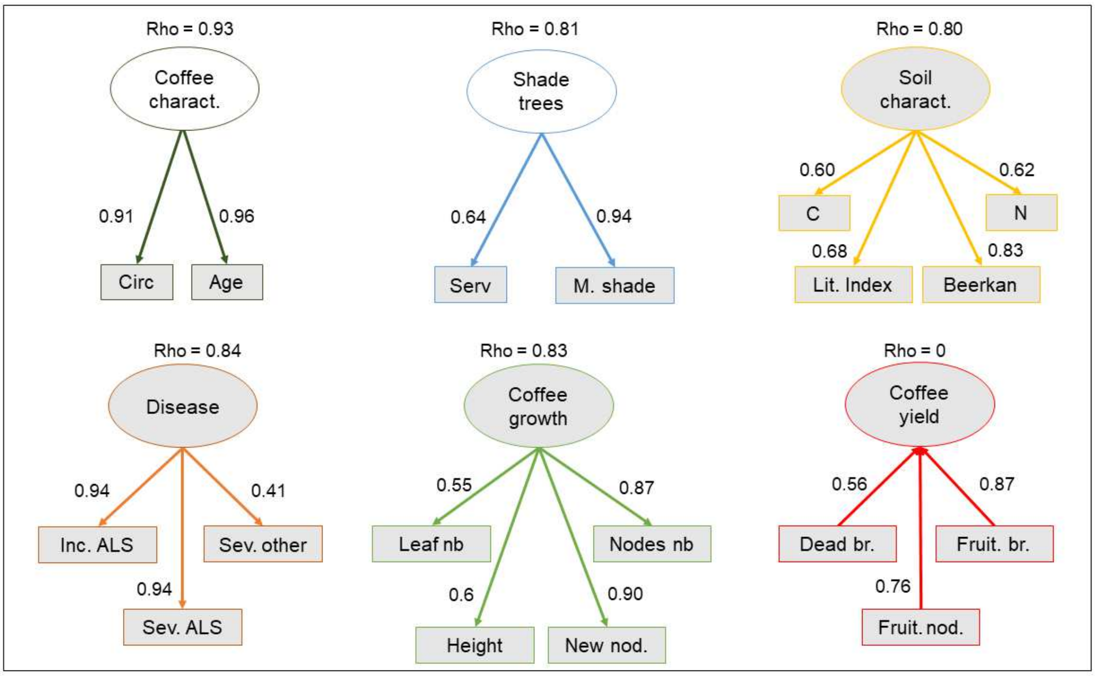

Figure 3. Results of the measurement model representing the six blocks with their latent variables (ovals) and observed variables (rectangles), and the correlation coefficient between each latent variable and the observed variables. Exogenous blocks are shown in white and endogenous blocks in grey. Reflective blocks are represented by arrows going from the latent to the observed variables, while the direction is reversed for formative blocks. The Dillon-Goldstein's rho values are shown above each block. Circ is the circumference of coffee plants; Age is age of coffee plants; Serv is the abundance of service trees; M. shade is the mean shade percentage; C is soil organic carbon; Lit. Index is the litter index; Beerkan is the Beerkan test results; N is soil nitrogen percentage; Inc. ALS is the ALS incidence; Sev. ALS is the ALS severity; Sev. Other is the severity of the other foliar diseases; Leaf nb is the number of leaves; Height is the height of coffee plants; New nod is the number of new nodes; Nodes nb is the number of nodes; Dead br is the number of dead branches, Fruit. Nod is the number of fruiting nodes; Fruit. Br is the number of fruiting branches.

4.4. Relationships between blocks

All endogenous blocks had an R^2 coefficient higher than 0.2, the diseases and 'coffee yield' latent endogenous variables had an R^2 coefficient of between 0.2 and 0.5, the 'soil characteristics' and 'coffee growth' latent endogenous variables had an R^2 higher than 0.5 (Fig. 4).

The 'soil characteristics' block was positively correlated with the 'shade trees' block (0.14), the 'coffee characteristic' block (0.74) and the 'coffee growth' block (0.19), but negatively correlated with ‘coffee yield’ (-0.08) and ‘diseases’ (-0.1). ‘Diseases’ was positively correlated with ‘coffee characteristics’ (0.33) and ‘shade trees’ (0.49).

The ‘coffee growth’ and ‘coffee yield’ blocks were negatively correlated with ‘diseases’ (-0.02; -0.12) and ‘shade trees’ (-0.25; -0.37).

The ‘coffee characteristics’ and ‘coffee growth’ had a positive correlation (0.54). The ‘coffee yield’ block was negatively correlated with the ‘coffee characteristics’ and ‘coffee growth’ blocks (-0.36; -0.06).

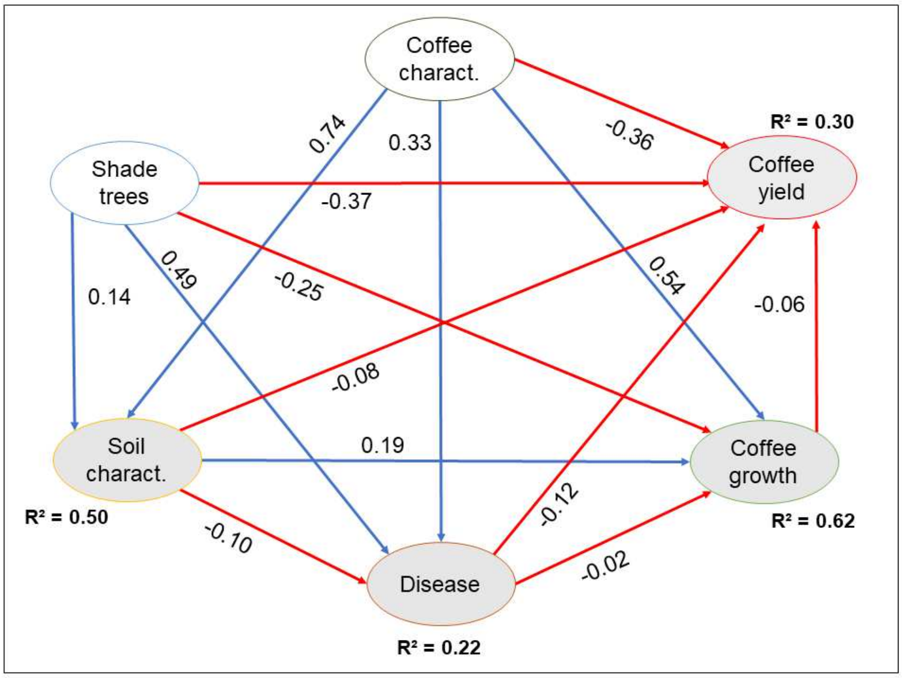

Figure 4. Results of the structural model representing the network of interactions between blocks, as shown by significant paths. Each arrow represents shade with its regression coefficient: blue arrows represent shade with a positive coefficient and red arrows with a negative coefficient. Endogenous blocks (grey) are also represented by their R^2 coefficient, with the coefficient being null for exogenous blocks (white).

4. DISCUSSION

4.1. ANALYSIS OF DIRECT EFFECTS AMONG THE SYSTEM COMPONENTS

The soil characteristics block (soil fertility proxy) was positively correlated with the shade tree block. This correlation meant that soil fertility was higher in plots with a larger shade percentage and with a greater number of N-fixing trees, confirming the findings of the recent study of Sauvadet et al. (2018). Indeed, the fertility under shade trees was increased by the N-fixation capacity of the service trees as well as by the shade tree pruning practices (Beer et al., 1997). The increased litter quality and quantity restored soil organic carbon and promoted the development of vital soil microorganisms like bacterial-feeding nematodes (Sauvadet et al., 2018). Most N-fixing tree species lose their leaves during the dry season; those leaves are fast decomposing materials that represent a source of C and nutrients for the soil (Tapia-Coral et al., 2005). Litter restitution thus improves and maintains the soil activity and fertility during this season, which is crucial for coffee production (Wintgens, 2004).

The diseases block was positively correlated with shade trees, thus highlighting their importance in disease management (Avelino et al., 2018). The model confirmed that ALS — a major component of the block — was favored by high shade which induces high humidity (Avelino et al., 2007). In addition, some species of the service tree group, especially *Inga* spp. were ALS hosts (Granados Montero, 2015) and could be a significant source of inoculum (Staver et al., 2001).

The negative correlation between shade trees and coffee growth and coffee yield suggested that reducing the canopy openness limits the light available for coffee growth (DaMatta, 2004). Shade trees were generating 49-85% shade (73% on average), which was much above the shade percentage found in most conventional coffee plantations. Although the effect of the shade percentage on coffee growth is still quite controversial, higher growth rates (up to the 40% threshold) are usually observed under shade (Charbonnier et al. 2017). In our case, all plots were equal or above this threshold and a negative effect of shade on coffee growth and yield was therefore expected.

The negative correlation between the ‘soil characteristics’ block and the ‘diseases’ block, indicated that coffee plants growing in more fertile soils are less affected by foliar diseases. Soil fertility could have induced a physiological resistance, as demonstrated with coffee rust (Toniutti et al 2017).

The positive relation observed between coffee characteristics (bigger and older coffee plants) and soil characteristics (fertility proxy) was probably related to the fact that soil quality was higher in older plantations. This could be explained by the acceleration of carbon cycle dynamics due to the increased organic matter input in the soil system, notably from litter fall linked to increased biotic activity, as demonstrated in rubber plantations (Thoumazeau et al, 2019b). Moreover, old coffee plants were more pruned in the previous year and pruning residue was left on the ground, thus increasing the soil organic matter (Gomez-Munoz et al. 2016). Pruning practices on older coffee plants could also explain why, despite the fact that they were growing on more fertile soils and had the better growth, they had the lowest berry production. Indeed, freshly pruned coffee plants first distribute their resources to promote growth (Charbonnier et al. 2017). The positive correlation between the coffee plant age and the disease incidence and severity illustrated that, besides their better growth and resistance related to high fertility, older coffee plants were more sensitive to foliar diseases.

As expected, foliar-diseases had a negative effect on coffee growth and yield. Foliar diseases reduced the leaf area available for photosynthesis process and did not allow plants to recover and sprout leaves or new nodes (Waller et al., 2007). Higher disease incidence and severity reduced fruiting production — this was the combined result of decreased photosynthesis and reduced redistribution of resources from leaves to fruits (Cerda et al., 2017).

4.2. Analysis of indirect effects of the system components on diseases, coffee growth and yield

Here we review the indirect and antagonistic effects highlighted by the PLS-PM model. First, a close relationship was noted between coffee characteristics, coffee growth and soil blocks. As discussed previously, the plots with higher fertility were associated with older coffee plants, which had higher growth due to the pruning practices. However, for the same reason, these coffee plants had the lowest berry production.

Although shade cover had antagonistic effects on the leaf diseases studied, with a high level of ALS but a low level of brown-eye spot (Avelino et al, 2018), we found that the shade trees favored foliar diseases overall. By increasing the soil fertility, they increased the coffee resistance, thereby reducing the disease incidence and severity. Moreover, the negative relationship between high shade cover and coffee growth and yield was direct but also indirect via the foliar diseases fostered by the shade trees. Conversely, high shade cover was also indirectly and positively related to high soil fertility, which increases the growth of coffee plants and reinforces their resistance (Toniutti et al. 2017).

Finally, coffee production resulted from a set of factors derived from the direct and indirect effects of all components. All effects within the agroecosystem must be taken into account to achieve balanced foliar disease management. It is now essential to quantify the trade-off between shade trees, soil characteristics, diseases, coffee growth and yield in order to improve overall agroecosystem management, and above all coffee production.

4.3. PLS-PM TO UNDERPIN FUTURE INITIATIVES AND PROSPECTS

The PLS-PM findings had a goodness-of-fit of about 0.5, which is an average value. We noted that all of the 'soil characteristics' and 'coffee growth' blocks were better explained than others. Inversely, the 'diseases' and 'coffee yield' blocks were less well explained than other blocks.

It would be interesting to integrate the herbaceous layer in the analysis so as to gain insight into the 'diseases' and 'coffee yield' blocks. Recent studies showed that this herbaceous layer also has an impact on the ALS incidence and severity (Granados Montero, 2015). The extent of the incidence and severity of the herbaceous layer would directly affect the incidence and severity of diseases on the coffee plants and indirectly the coffee yield via a direct impact on dead branches. Adding the secondary loss, i.e. dead branches, in 2016 directly affected the number of available berry producing branches in 2017.

In future studies, it would also be interesting to integrate coffee growth from previous years to take the biannual resource allocation of coffee plants into account. Another improvement would be to integrate temperature fluctuations and precipitation patterns, which have a marked impact on coffee tree growth and production (Charbonnier et al., 2017), as well as on the degree of ALS incidence and severity (Avelino et al., 2007), but that will require larger datasets.

5. CONCLUSION

PLS-PM enabled us to study the network of interactions occurring within the agroecosystem, including antagonistic effects of shade trees. First, shade trees had a negative effect on coffee growth and yield and increased the foliar diseases incidence and severity, and secondly, they increased soil fertility which in turn decreased the disease prevalence and increased coffee growth. This holistic approach regarding the role of trees in the ecosystem highlighted the need to consider the shade percentage quantitatively (an excess or lack of shade negatively impacted coffee growth and yield). It will be essential to assess the trade-offs between shade management, soil quality, disease regulation and yield gain when designing cropping systems that optimize shade cover.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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