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1 **Analysis of interactions amongst shade trees, coffee foliar**
2 **diseases and coffee yield in multistrata agroforestry**
3 **systems**

4
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21

22 **Abstract**

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

45

46 **Keywords**

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

49

50 1. INTRODUCTION

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

64
65 Nicaragua is eighth largest *C. arabica* producing country in the world, with production
66 reaching 2.54 million kg in the 2017-2018 cycle. Coffee cropping has a huge socioeconomic
67 impact in this country, where 44 thousand coffee producers cultivate a total area of 1.5
68 million ha. Most of the farms grow coffee under agroforestry systems, and 97% of them are
69 less than 14 ha. Nicaraguan coffee-based agroforestry systems are known to be particularly
70 complex with a remarkable diversity of shade trees (Hagggar et al., 2015). This diversity
71 includes species that produce goods for local markets, native forest species that are grown
72 mainly for timber, along with service tree species — mostly Fabaceae — that are planted to
73 provide shade while improving soil fertility and crop system sustainability (Barradas and
74 Fanjul, 1986; Vaast et al., 2005). The coffee rust outbreak that occurred in 2013–2014 led
75 farmers to replace the rust-sensitive cv. Caturra plants in their coffee plantations with rust-
76 resistant cv. Catimor plants (Libert Amico et al., 2019). However, Catimor cultivars are

77 particularly sensitive to the American leaf spot (ALS) disease caused by *Mycena citricolor*
78 (Sequeira 1958; Staver et al., 2001; Allinne et al., 2016). Other diseases like brown-eye spot
79 (*Cercospora coffeicola* Berk. & Cooke), anthracnose (*Colletotrichum* sp.) and coffee thread
80 blight (*Corticium kolegora*) also affect cv. Catimor coffee plants (Waller et al., 2007). These
81 foliar diseases have negative effects on coffee growth and production, and interact with each
82 other as a disease complex depending on the coffee crop status and the microclimatic
83 conditions. A major way to improve disease management is to integrate the role of shade
84 trees on these foliar diseases (Avelino et al., 2018; Allinne et al., 2019). Indeed, ALS and
85 coffee thread blight are favored by high humidity when shade levels are elevated, unlike
86 brown-eye spot and anthracnose that tend to affect sun-grown coffee plants (Staver et al.,
87 2001; Muller et al., 2008; Bedimo et al., 2012). Most Nicaraguan farmers do not have
88 sufficient financial resources to manage pests and diseases using pesticides (Bro et al.,
89 2019). Understanding the relations within disease complexes that affect coffee plants and the
90 diversity of shade trees is crucial and requires an overview of the entire pathosystem.

91
92 In these complex agroforestry systems, shade trees do not just provide shade to the crop
93 system, they also have directly impact coffee growth and yield by increasing the leaf surface
94 and coffee quality (Vaast et al., 2005; Charbonnier et al., 2017). Conversely, shade trees and
95 coffee plants can compete for light and nutrients, especially under high shade tree density
96 conditions (Charbonnier et al., 2013). However, shade trees may also markedly alter the soil
97 characteristics, and in some cases improve soil fertility (Sauvadet et al., 2018). This is well-
98 known by farmers who often plant nitrogen-fixing trees (e.g. *Inga* spp.) to favor nitrogen
99 fixation (Cerdán et al., 2012). These interactions between shade trees and agroecosystem
100 processes are also driven by farmers through their pruning practices whereby the canopy is
101 opened and dead branches are left on the ground (Cerdán et al., 2012). This litter addition
102 around coffee plants may enhance soil fertility and promote the activity of beneficial soil
103 microorganisms (Sauvadet et al., 2018). Coffee plant resistance against foliar diseases is
104 dependent on these soil characteristics. Indeed, coffee plants growing in more fertile soil

105 have higher regeneration properties and growth, which are key physiological resistance
106 factors (Ratnadass et al., 2012). Soil fertility also influences the quality and abundance of
107 coffee beans produced (Barel and Jacquet, 1994; Lin, 2010).

108
109 New tools are needed to study this network of interactions between different agroecosystem
110 components overall. We used a structural equation modelling (SEM) approach called partial
111 least square path modelling (PLS-PM) to gain further insight into the direct and indirect
112 effects of shade trees on coffee foliar diseases and coffee yield in Nicaraguan coffee-based
113 agroforestry systems.

114

115 **2. MATERIAL AND METHODS**

116 **4.2. STUDY SITES**

117 The study took place in the Matagalpa region (Nicaragua's main coffee production area) near
118 the village of El Tuma-La Dalia. We studied three small coffee farms from May 2016 to
119 February 2018 under conventional, low-input and organic disease management conditions.
120 The farms were chosen for their high shade tree diversity, with marked variability in the
121 proportion of shade, i.e. 49-85% (Table 1). These farms only grew non-certified *Coffea*
122 *arabica* (Rubiaceae) cv. Catimor plants. This genetic material was rust resistant (no evidence
123 of rust affection was observed during the experiment) but sensitive to American leaf spot
124 caused by *Mycena citricolor* (Allinne et al., 2016; Libert Amico et al, 2019). The farms were
125 located between 13°02'67.7"N and 13°08'75.6"N and between 85°61'42.7"W and
126 85°71'48.3"W, within a similar elevation range (650-850 m a.s.l.). The mean annual
127 temperature was 23°C, with annual precipitation ranging from 2,000 to 2,600 mm. The rainy
128 season in this region is between May and December (Amores Contreras, 2015).

129 Table 1. Description of the three farms where the study was conducted in the area around El Tuma-La
130 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 rainfall	(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 management	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)

131

132 4.3. AGROFORESTRY SYSTEM CHARACTERIZATION

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

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

143

144 **4.3.1. SHADE TREE CHARACTERIZATION**

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

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

155

156 We took hemispherical pictures to characterize the shade percentage at four different times:
157 November 2016, February 2017, June 2017 and September 2017. Hemispherical pictures
158 were taken above all selected coffee plants with a Nikon Coolpix 4500 equipped with a
159 fisheye converter (FC-E8 0.21x). These pictures were analyzed using Gap Light Analyzer
160 (GPA-V2) software to assess the shade percentage above each coffee tree (Frazer et al.,
161 1999). The annual mean shade percentage was used for the analysis.

162

163 **4.3.2. COFFEE TREE CHARACTERIZATION**

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

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

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

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

181

182 4.3.3. COFFEE FOLIAR DISEASE CHARACTERIZATION

183 The measured foliar disease complex encompassed American leaf spot (ALS; *Mycena*
184 *citricolor*), brown-eye spot (*Cercospora coffeicola* Berk. & Cooke), anthracnose
185 (*Colletotrichum* sp.) and coffee thread blight (*Corticium kolegora*). We measured the severity
186 (i.e. the percentage of diseased leaves) and the incidence (i.e. the percentage of leaf area
187 affected by diseases) of these diseases on three branches of selected coffee plants. As ALS
188 is a major foliar disease, we decided to treat it separately from other diseases to gain clear
189 insight into the relationship between the agrosystem and the ALS incidence and severity. We
190 separately integrated ALS variation patterns and those of other diseases by calculating the
191 relative AUDPC based on the measurements obtained at four dates (May 2017, September
192 2017, December 2017, February 2018), which represented a complete disease development
193 cycle.

194

195 4.3.4. SOIL CHARACTERIZATION

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

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

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

211

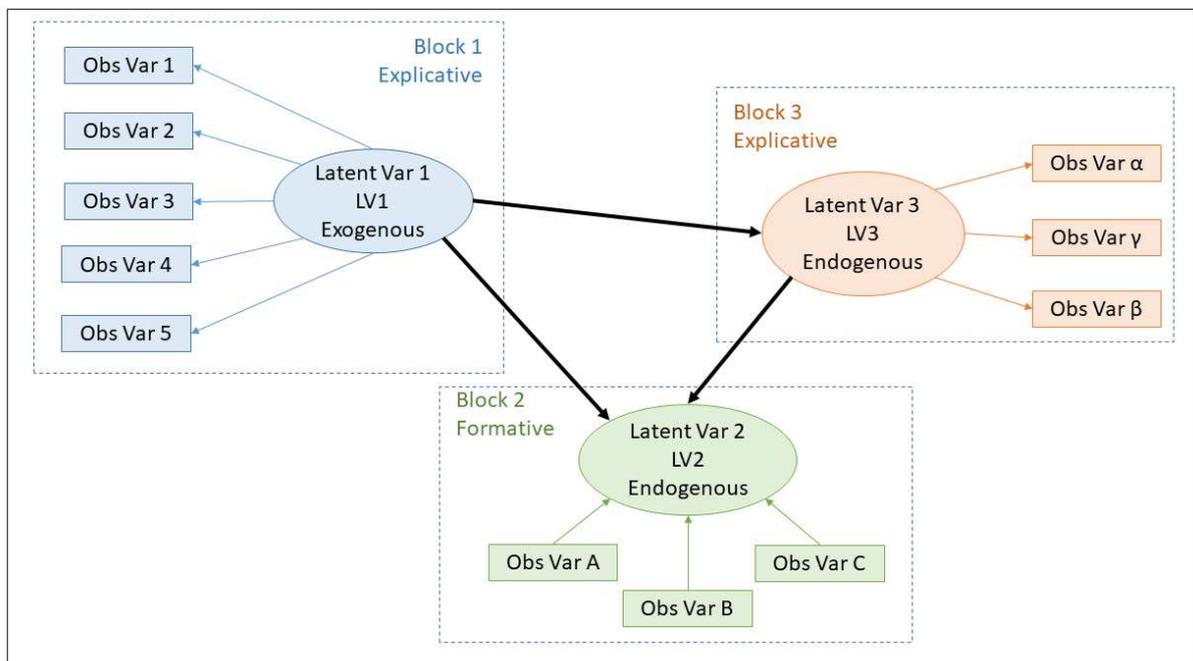
212 **4.4. STATISTICAL ANALYSIS**

213 Structural equation modelling (SEM) is particularly appropriate for gain insight into
214 interactions between shade trees, soil, diseases and coffee plants. SEM analyses are able to
215 explain relationships between observed variables by clustering them as latent variables
216 representative of common concepts. Structural equation modelling analyses can be used to
217 understand complex systems (Hoyle, 2012; Vinzi and Trinchera, 2013) and was successfully
218 applied to analyse ecological regulations in agroforestry systems in banana and cocoa
219 plantation settings (Poeydebat et al. 2017; Oliveira et al., 2018). This type of analysis is
220 divided into two main types: the SEM-ML method based on the maximum likelihood (ML) and
221 the partial least square path modelling (PLS-PM) method based on simple regressions to
222 explain the latent variables (Vinzi and Trinchera, 2013). The PLS-PM method was

223 specifically chosen for its flexibility to manipulate datasets with numerous variables, and its
224 capacity to represent clearly complex interaction systems.

225

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



232

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

237

238 4.5. MEASUREMENT MODEL BUILDING

239 Our measurement model contained six blocks including latent variables corresponding to the
240 measurement domains presented earlier, i.e. inherent coffee characteristics (hereafter simply

241 called 'coffee characteristics'), shade trees, soil characteristics, foliar diseases, coffee growth
 242 and coffee yield (Table 2). We built three blocks related to coffee plants because we
 243 assumed that these blocks represent a specific aspect of coffee plants, and influence each
 244 other. Each block was composed of a latent variable and its related observed variables
 245 (Table 2). According to the method described by Sanchez (2013), the coffee characteristics,
 246 shade trees, soil characteristics, foliar diseases and coffee growth blocks were **reflective**
 247 because the variables observed inside each block were well correlated. Indeed, for each
 248 **reflective block**, observed variables have to move in the same direction, and when a variable
 249 increases or decreases, the others change in the same way (Sanchez, 2013). We verified
 250 this condition by examining the unidimensionality of these blocks with Dillon-Goldstein's rho.
 251 A block is unidimensional when its rho value is higher than 0.7 (Sanchez, 2013).

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

256
 257 Table 2. Description of blocks represented by their latent variable and observed variables. **ALS is**
 258 **American leaf spot of coffee; organic C is soil organic carbon; N is the nitrogen percentage; iron (Fe),**
 259 **potassium (K), magnesium (Mg), and phosphorus (P) are in ppm; CEC is the cation exchange**
 260 **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

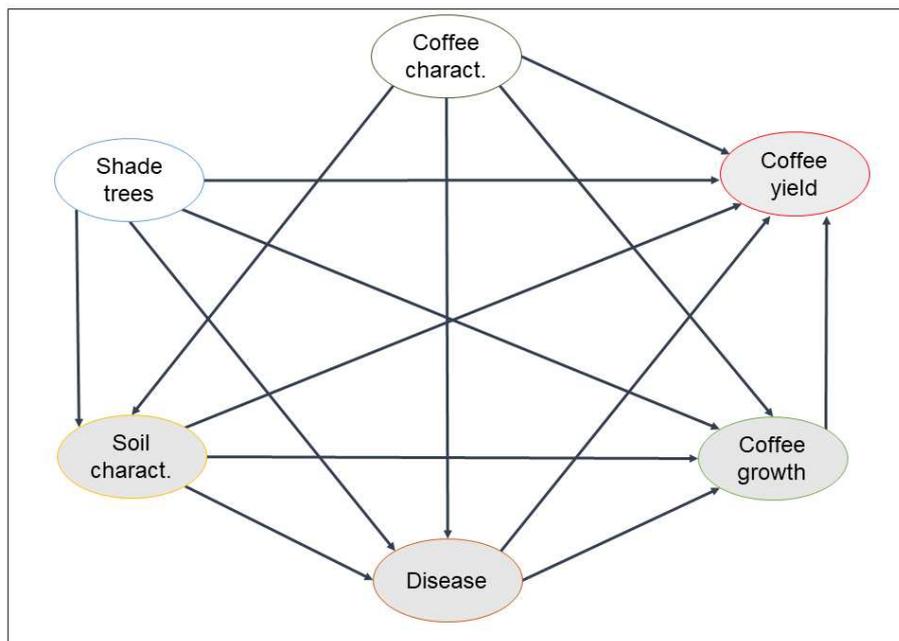
261

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

266

267 4.6. STRUCTURAL MODEL BUILDING

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



273

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

277

278 In order to validate our block, the PLS-PM model was used to calculate the R^2 coefficient of
279 each exogenous block that expressed the explained variability for each block. Other latent
280 variables better explained the block when the R^2 coefficients were high. The model

281 parameters were thus adjusted to have R^2 coefficients higher than 0.2, which is a moderately
282 low value (Sanchez, 2013).

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

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

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

288

289 **3. RESULTS**

290 **4.1. CLUSTERING OF SHADE TREES**

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

298

299 **4.2. PLS-PM MODEL OUTPUT**

300 The measurement model and structural model results shed light on the complex network of
301 interactions between shade trees, coffee plants, foliar diseases and soil characteristics.
302 While the measurement model showed the block compositions, the structural model revealed
303 the strength of the relation between them. The overall PLS-PM had a goodness-of-fit of
304 0.4971.

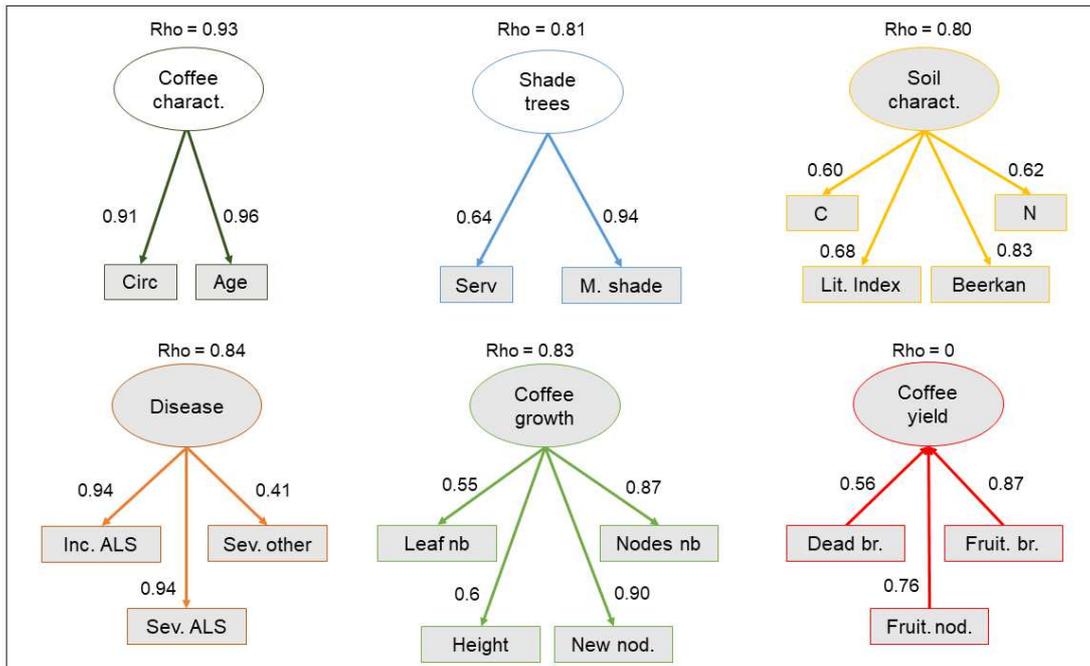
305

306 **4.3. RELATIONSHIPS BETWEEN THE OBSERVED AND ASSOCIATED LATENT VARIABLES (WITHIN** 307 **BLOCK)**

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

315 The 'coffee characteristics' latent variable was well-explained by its two observed variables,
316 i.e. age (0.96) and circumference (0.91) (Fig. 3). From the 'shade trees' block, only the
317 observed variables of the mean shade percentage (M. shade, 0.94) and service group (Serv,
318 0.64) had a significant impact. The 'soil characteristics' latent variable was explained only by
319 the Beerkan test (0.83), organic carbon quantity (0.6) and nitrogen percentage (0.62), as well
320 as the litter index (0.68). The 'soil characteristics' parameter thus represented the soil fertility.
321 The 'diseases' block was mainly explained by the observed variables related to ALS severity
322 (0.94) and ALS incidence (0.94). The remaining observed variables that explained the 'coffee
323 growth' block were the height (0.6), number of nodes (0.87), number of new nodes (0.9) and
324 number of leaves (0.55). Inside the 'coffee yield' block, the number of fruiting branches per
325 tree was more significant (0.87), it was correlated with the number of fruiting nodes (0.76) per
326 branch and with the number of dead branches (0.56).

327



328

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

341

342 4.4. RELATIONSHIPS BETWEEN BLOCKS

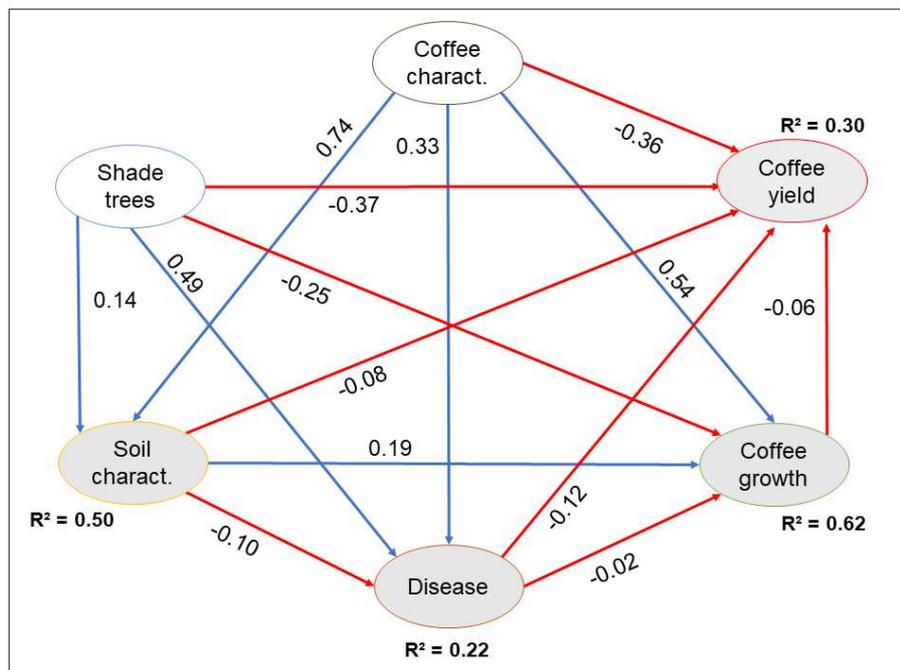
343 All endogenous blocks had an R^2 coefficient higher than 0.2, the diseases and 'coffee yield'
 344 latent endogenous variables had an R^2 coefficient of between 0.2 and 0.5, the 'soil
 345 characteristics' and 'coffee growth' latent endogenous variables had an R^2 higher than 0.5
 346 (Fig. 4).

347 The 'soil characteristics' block was positively correlated with the 'shade trees' block (0.14),
 348 the 'coffee characteristic' block (0.74) and the 'coffee growth' block (0.19), but negatively

349 correlated with 'coffee yield' (-0.08) and 'diseases' (-0.1). 'Diseases' was positively correlated
 350 with 'coffee characteristics' (0.33) and 'shade trees' (0.49).

351 The 'coffee growth' and 'coffee yield' blocks were negatively correlated with 'diseases' (-0.02;
 352 -0.12) and 'shade trees' (-0.25; -0.37).

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



356
 357 Figure 4. Results of the structural model representing the network of interactions between blocks, as
 358 shown by significant paths. Each arrow represents shade with its regression coefficient: blue arrows
 359 represent shade with a positive coefficient and red arrows with a negative coefficient. Endogenous
 360 blocks (grey) are also represented by their R² coefficient, with the coefficient being null for exogenous
 361 blocks (white).

362

363 4. DISCUSSION

364 4.1. ANALYSIS OF DIRECT EFFECTS AMONG THE SYSTEM COMPONENTS

365 The soil characteristics block (soil fertility proxy) was positively correlated with the shade tree
 366 block. This correlation meant that soil fertility was higher in plots with a larger shade

367 percentage and with a greater number of N-fixing trees, confirming the findings of the recent
368 study of Sauvadet et al. (2018). Indeed, the fertility under shade trees was increased by the
369 N-fixation capacity of the service trees as well as by the shade tree pruning practices (Beer
370 et al., 1997). The increased litter quality and quantity restored soil organic carbon and
371 promoted the development of vital soil microorganisms like bacterial-feeding nematodes
372 (Sauvadet et al., 2018). Most N-fixing tree species lose their leaves during the dry season;
373 those leaves are fast decomposing materials that represent a source of C and nutrients for
374 the soil (Tapia-Coral et al., 2005). Litter restitution thus improves and maintains the soil
375 activity and fertility during this season, which is crucial for coffee production (Wintgens,
376 2004).

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

383 The negative correlation between shade trees and coffee growth and coffee yield suggested
384 that reducing the canopy openness limits the light available for coffee growth (DaMatta,
385 2004). Shade trees were generating 49-85% shade (73% on average), which was much
386 above the shade percentage found in most conventional coffee plantations. Although the
387 effect of the shade percentage on coffee growth is still quite controversial, higher growth
388 rates (up to the 40% threshold) are usually observed under shade (Charbonnier et al. 2017).
389 In our case, all plots were equal or above this threshold and a negative effect of shade on
390 coffee growth and yield was therefore expected.

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

395

396 The positive relation observed between coffee characteristics (bigger and older coffee plants)
397 and soil characteristics (fertility proxy) was probably related to the fact that soil quality was
398 higher in older plantations. This could be explained by the acceleration of carbon cycle
399 dynamics due to the increased organic matter input in the soil system, notably from litter fall
400 linked to increased biotic activity, as demonstrated in rubber plantations (Thoumazeau et al,
401 2019b). Moreover, old coffee plants were more pruned in the previous year and pruning
402 residue was left on the ground, thus increasing the soil organic matter (Gomez-Munoz et al.
403 2016). Pruning practices on older coffee plants could also explain why, despite the fact that
404 they were growing on more fertile soils and had the better growth, they had the lowest berry
405 production. Indeed, freshly pruned coffee plants first distribute their resources to promote
406 growth (Charbonnier et al. 2017). The positive correlation between the coffee plant age and
407 the disease incidence and severity illustrated that, besides their better growth and resistance
408 related to high fertility, older coffee plants were more sensitive to foliar diseases.

409

410 As expected, foliar-diseases had a negative effect on coffee growth and yield. Foliar
411 diseases reduced the leaf area available for photosynthesis process and did not allow plants
412 to recover and sprout leaves or new nodes (Waller et al., 2007). Higher disease incidence
413 and severity reduced fruiting production — this was the combined result of decreased
414 photosynthesis and reduced redistribution of resources from leaves to fruits (Cerdeira et al.,
415 2017).

416

417 **4.2. ANALYSIS OF INDIRECT EFFECTS OF THE SYSTEM COMPONENTS ON DISEASES, COFFEE** 418 **GROWTH AND YIELD**

419 Here we review the indirect and antagonistic effects highlighted by the PLS-PM model. First,
420 a close relationship was noted between coffee characteristics, coffee growth and soil blocks.
421 As discussed previously, the plots with higher fertility were associated with older coffee

422 plants, which had higher growth due to the pruning practices. However, for the same reason,
423 these coffee plants had the lowest berry production.

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

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

437

438 **4.3. PLS-PM TO UNDERPIN FUTURE INITIATIVES AND PROSPECTS**

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

443 It would be interesting to integrate the herbaceous layer in the analysis so as to gain insight
444 into the 'diseases' and 'coffee yield' blocks. Recent studies showed that this herbaceous
445 layer also has an impact on the ALS incidence and severity (Granados Montero, 2015). The
446 extent of the incidence and severity of the herbaceous layer would directly affect the
447 incidence and severity of diseases on the coffee plants and indirectly the coffee yield via a

448 direct impact on dead branches. Adding the secondary loss, i.e. dead branches, in 2016
449 directly affected the number of available berry producing branches in 2017.

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

456

457 **5. CONCLUSION**

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

467

468 **CONFLICTS OF INTEREST**

469 The authors declare that they have no conflicts of interest.

470

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478

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