Pest-regulating networks of the coffee berry borer (*Hypothenemus hampei*) in agroforestry systems

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Abstract

Pest regulation in agroforestry systems (AFS) is beginning to be well-recognized, but the mechanisms implied in the interaction network between the environment, pests and predators in AFS are still not well-described. The aim of this work is to understand how plant diversity associated with AFS regulates the coffee berry borer (CBB) taking into account a tripartite interaction network: pest–predator–environment. It further seeks to understand how farmers' management practices can modify the regulating network. Using field data from coffee-based AFS and structural equation modeling, we assessed the effects of environmental conditions (% shade cover, tree area surface, coffee density) and farm management (conventional, integrated, organic) on (1) ant predatory groups, (2) the abundance and the damage from CBB and (3) their interactions. Percentage of shade cover was positively correlated to CBB initial infestation (through direct effect) and negatively through its effect on coffee phenology. A higher percentage of shade is also negatively related to damage intensity. Farmers' practices significantly reduced the CBB population without considerable side effects on the ant predatory group, probably due to the high plant diversity within these farms. The abundance of the most diversified ant predatory group has a top-down effect on the peak of the CBB infestation rate. Our approach appears promising for a better understanding of the complex regulating network in coffee AFS and confirms the importance of an integrated management strategy to reduce CBB damage.

Key words: top down regulation, bottom up regulation, integrated pest management, biodiversity

1 Introduction

Coffee (*Coffea* spp., L. (Gentianales: Rubiaceae)) is an important cash crop and international commodity supporting ~25 million people globally (FAO2015) most of them being smallholders (farming less than 10 ha) in rural areas of tropical developing countries. In Central America (including Mexico) the production of coffee mainly Arabica coffee *(Coffea arabica* L.), is around 21.35 million 60-kg bags representing 12.6% of total production by exporting countries (ICO, 2019). In this region, total areas cultivated with this crop represent 1.79 million ha in 2017 over the 10 million ha in the world (FAO 2017). Nicaragua is the third country (after Honduras and Mexico) for coffee production and as coffee exporter in Central America.

Arabica coffee is usually produced in small agroforestry systems (AFS), traditionally under a dense shade canopy with a great variety of management types, from systems resembling natural forest (Moguel and Toledo, 1999) to monospecific intensive systems. Coffee-based AFS provide ecosystemic services to the producers (Cerdán et al., 2012), including pest and disease regulation.

Plant diversity in AFS can provide different regulation pathways, driven by predation (top-down) or by resources (bottom-up), to regulate pest populations and to reduce damage and losses induced. This regulation network is the result of complex biotic and abiotic interacting components, allowing an endogenous regulation of several potential pest species (Vandermeer et al., 2010)**.** Environmental factors in AFS associated with the composition of plant diversity may alter pest regulation by modifying the development, reproduction and foraging behavior of the pest. Resource availability and microclimatic conditions are two main mechanisms that drive the impact of plant diversity on pests and diseases in AFS (Gidoin et al., 2014). Through its effects on microclimate, shade can directly affect processes (development time, percentage of survivorship, sex ratio) related to the life cycle of the pest (Beer et al., 1997; Schroth et al., 2000). The variability in resource availability created by plant diversification can also impact pest regulation (Avelino et al., 2011). The tree layer may also constitute a barrier to pest dispersal or act as a dilution element, decreasing host plant density (Schroth et al., 2000). Vegetation richness can indirectly affect pests by supplying a large diversity of habitats that favors higher natural diversity of predators, which occupy several or different niches (Letourneau et al., 2011), resulting in a better pest regulation. Many studies describe the effects of management or of environmental factors or of natural enemies on pest populations, but only few studied the effect of a combination of factors on those populations (Poeydebat et al., 2017, Teodoro et al., 2008). As a result, the interaction network between the environment, pests and predators in AFS are still not well-described.

Here, we proposed to study this regulation network, focusing on regulation of the most important coffee pest in the world, the coffee berry borer (CBB), *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae), within coffee AFS. Yearly losses caused by coffee berry borer have been estimated at USD 500 million (Vega et al., 2015). Regarding its biology, the entire life cycle of the CBB depends on coffee fruits. Adult females dig a hole in the coffee berry and lay eggs in internal galleries. Then larvae and adults feed on the coffee seed until the females emerge from the fruit (Damon, 2000). The seed quality is reduced, making them less suitable for the market (Wegbe et al., 2003). If appropriate control measures are not implemented, infested coffee berries can lose weight up to 50% (Montoya et al. 1999) meaning that a farmer could lose almost half of its production under severe attacks.

Several strategies have been conducted to manage CBB around the world (Aritzabal et al., 2016; Vega et al., 2015). Chemical insecticides (*e.g.*, endosulfan, chlorpyrifos, cypermethrin) are quite effective to control CBB. But since, 2011 the use of endosulfan (the most commonly used and effective insecticide) is being questioned due to its toxicity and persistence (Mrema et al., 2013). Farmers of Latin American countries continue to use this chemical insecticide but the tendency is decreasing due to international rules and alternative strategies are explored (UK PAN, 2015). Some farmers used microbial insecticides (*i.e., Beauveria bassiana*) but their actions are limited to migratory periods (Aritzabal et al. 2016). An integrated management is recommended for CBB management that combines harvest of the remaining fruits (postharvest sanitation), shade tree pruning and trapping (semiochemical substances) (Aristizabal et al., 2016, Johnson et al., 2019). In different countries of Latin America, CBB regulation by parasitoids was investigated following their introduction from their African native region (reviewed by Aristizabal et al., 2016). The action of more generalist natural ennemies, in particular ants, on CBB regulation have been widely studied (Morris et al. 2018). This regulation can occur through several mechanisms and in different biological stages (Morris and Perfecto, 2016; Morris et al., 2018)). Predation can happen while CBBs bore into coffee berries (Philpott et al., 2008a) or small ants can readily enter CBB holes in berries and remove larvae and pupae from their galleries (Morris and Perfecto, 2016). Infestation reduction can also occur through non-consumptive effects (preventing CBB from accessing the coffee fruits by interference competition, exclusion behavior). For instance, *Azteca instabilis* (Smith, 1862) was described in Mexico as one of the key regulator of CBB populations in coffee plantations (Perfecto and Vandermeer, 2006; Vandermeer et al., 2010). Gonthier et al., (2013) also showed that a diversified community of ant species decrease CBB colonization (to around 50% pooling all ants species together) in ant exclusion experiments. Other authors proved that the insectivore bird community in the AFS can also significantly contribute to CBB regulation (reduction around 5 to 10%) (Martínez-Salinas et al., 2016).

The efficiency of these regulation strategies rely both on biotic and abiotic interactions within the coffee systems. Environmental conditions created by associated biodiversity can either influence pest regulation directly, through a bottom-up effect, or indirectly, by modifying biotic interactions that promote top-down regulation by natural enemies. However, most studies about CBB regulation in coffee systems focus on the impact of one or few factors on a single response. Possible inferences from other factors are not considered and this often leads to many contradictory results. This is particularly true with the effect of shade cover (Soto-Pinto et al., 2002, Vega et al. 2015) or ant predation on CBB (Morris and Perfecto, 2016). Characterizing a regulating service in AFS involves integrating different components of the system to appreciate indirect effects that would not be detected when studying a single response variable.

The aim of this work is to understand how plant diversity associated with AFS regulates CBB taking into account a tripartite interaction network (pest–predator–environment). It further seeks to understand how farmers' management practices can modify the regulating network. Given ant dominance (biomass, diversity) in tropical ecosystems, evaluation of the regulating service will be illustrated by focusing on ant–CBB interaction. Based on assumptions from the conceptualization and knowledge of the studied agrosystem, we analyzed the relationships between CBB infestation, predatory ant abundance, environmental factors of AFS and management practices. We hypothesized that (1) some environmental conditions created by AFS have positive bottom-up effects that increase predatory ant abundance and, in return, (2) predatory ant abundance reduces CBB infestation through top-down effects and (3) some environmental conditions created by AFS have bottom-up effects on CBB infestation. We assessed how management practices affect the tripartite interaction by modifying densities of pest and predator communities and how the tripartite network and the management practices influence the damage on coffee berries.

2 Materials and methods

2.1 Site description

Trial sites were located near El Tuma–La Dalia (Matagalpa, Nicaragua). This province accounts for 28% of the country's coffee production (Bolaños, 2015). The coffee flowering period begins at the end of the dry season (March–April) and harvest runs from October to December. Field studies were conducted in three family coffee (*Coffea arabica*) farms (< 3.5 ha each) located between 650 and 850 m above sea level and characterized by different trees-species richness (Table 1) and by different management practices: a conventional farm (13°01'36.4''N 85°40'48.0''N), an organic farm (13°02'14.5''N 85°42'53.44''W) and a integrated farm (13° 05' 15.2'' N 85° 36' 51.4" W). Distance between the farms varied from 4.9Km to 11.8Km. CBB was controlled mainly with Endosulfan (one to two applications per season, around July when first berries start to suffer attack, $1L.ha^{-1}$) and occasionally with Cypermethrin until 2016 in the conventional farm, with *B. bassiana* (use of local strain) in the integrated farm and without any inputs in the organic farm (Table 1). Post harvest sanitation was conducted every year in the integrated and the organic farms.

2.2 Plot characteristics

Within each farm, 20 experimental units, consisting of a circular unit around a remarkable central plant, were monitored from May 2016 to October 2018. The central plant was chosen randomly among three common species (*Cordia alliodora; Inga oerstediana* and *Musa spp*) and other plant species (that could be different between), creating four different situations, with five replicates for each. Each experimental unit was circular, with a radius of 15 m and the distance between each unit was around 20m on average. In our study, we considered a sub-unit of 7 m radius (called plot hereafter) for data analysis. Four coffee trees were selected randomly for the monitoring within a radius of 5 m around the central plant in the plot. Due to severe pruning by the farmer at the end of 2017, only nine units were retained in the integrated farm. Forty-nine plots and 196 coffee trees were therefore monitored during the survey.

Within each plot, five environmental variables were characterized in 2017: percentage of shade cover (%SC), tree species richness, tree surface area (TSA), mean maximal temperature and coffee density (CD) (Table 1). The %SC received by each selected coffee tree within the plot was characterized by estimating canopy openness with hemispherical photographs taken with a Nikon Coolpix 4500. Photographs were taken in the morning between 5:30 a.m. and 7 a.m.and were analyzed using the Gap Light Analyzer in November 2016 and in February, June and September 2017. An average annual shade cover based on these four dates was therefore considered to approximate the %SC in the plots. The number of tree species that

Farm id	Farm level		Environmental variables (Plot level)				
	Management strategies	Species Richness	% shade cover	Associated tree richness	Max. temperature (°C)	Coffee density (/m²)	Tree surface (m²)
Conventional	Chem Insect, Fungicide, Herbicide, Chem. Fert.	38	79.98 (70.93-85.49)	4.75 (2-8)	27.83 (25.61-32.44)	133.65 (96-168)	0.37 (0.03-0.31)
Integrated	*B. bassiana,* Phyto. Harv., Fungicide, Herbicide, Chem. Fert.,	21	71.97 (62.48-77.29)	4.22 (2-10)	29.23 (27.25-33.39)	136.78 (96-168)	0.26 (0.03-0.59)
Organic	Phyto. Harv., Hom. Fert.	18	65.83 (49.05-76.10)	3.3 (1-7)	29.42 (26.68-32.75)	132.75 (97-179)	0.19 (0.02-0.50)

Table 1. Farm management strategies, species richness within farms and environmental variables at plot levels in the three selected farms. (Sp richn: tree species richness; Chem. Insect: Chemical Insecticide; Chem. Fert.: Chemical Fertilizer; Phyto. Harv.: Phytosanitary Harvest; Hom. Fert.: Homemade Fertilizer)

were equal or larger than the average height of coffee plants present in the plot were counted once to approximate the tree species richness. TSA per plot was determined by summing the surfaces of the associated trees calculated from the diameter at breast height measurement. Air temperature was recorded every hour from 09 May to 10 July 2017 in each plot using iButton™ data logger probes hung to a coffee tree. A mean maximal temperature per plot was evaluated as the average maximal temperature measured over the monitoring period. The number of coffee trees within the plot was also counted to estimate CD (Table 1).

2.2.1 Coffee berry borer (CBB) monitoring

2.2.1.1 CBB infestation rate

To estimate CBB infestation rate per coffee tree, the total number of fruits, suitable fruits (mature enough to be infested (Mariño et al., 2016)) and CBB-infested fruits (with a characteristic hole in its apex) were counted twice in 2018 at the beginning of the fruiting season (April 2018) and at the fruit peak season (October 2018) on three branches (on the upper part, on the middle part and on the lower part) of the selected coffee trees. The proportion of fruits infested by CBB per plot per date (IniCBB: CBB infestation at the beginning of the fruiting season; PeakCBB: CBB infestation at the fruit peak season) was determined by dividing the number of infested berries by the total number of suitable berries on the four coffee trees (Trujillo et al., 2006).

2.2.1.2 CBB adult population

We also monitored CBB adult population (AdCBB) in March 2018 during the migratory flights thanks to artisanal attractive traps. We wanted to evaluate adult population at this particular to see the effect of environmental conditions on settlement of initial population in the plots. Settling down phase is characterized by the movement of the population from fruit of the previous season towards the first maturing fruits and correspond to the second flying peak activity (Aristizábal et al., 2017, Matthieu et al. 1998, Messing et al., 2012). We also hypothesized that this adult population can be a good indicator of initial infestation rate in the plots. One trap was installed 1.20 m above the ground on one coffee plant per plot (Dufour and Frérot, 2008). The traps were made using a 2-liter plastic bottle modified with three openings in the upper part for insect entrance and with a recipient part at the bottom filled with water and three drops of chlorine for insect collection. The attractive mixture, containing a combination of methanol-ethanol (1:1 volume) (Dufour and Frérot, 2008), was slowly and continuously diffused thanks to a syringe placed in the middle of the bottle (that needs to be refilled every month). CBB adult populations in the plot were estimated by calculating the mean number of individuals caught in the trap over six days during three weeks.

2.2.1.3 Severity of the damage

In each plot, 100 infested cherries were sampled in October 2018 on the coffee trees. The cherries were subsequently cut in two in the laboratory to assess the presence or absence of females inside the fruit and to evaluate the severity of the damage. Three scores of damage were attributed to each cherry: 0 for no damage on the beans, 1 for partly damaged (half of the berry affected) and 2 for highly damaged (at least three-fourths of the berry affected).

2.2.2 Ant monitoring and classification

Ants were sampled on selected coffee trees and on the central plant three times during one year to be representative of different climatic conditions (dry season, and two rainy season, in the end of September 2017, January 2018 and April 2018), following two different sampling methods. One was to collect all ants observed on a plant during five minutes, using a brush. At the same time, a canned tuna–honey bait (90% of honey and 10% of tuna) was deposited on a coffee leaf at about 30 centimetres above the ground and all ants observed at baits after 25 minutes were collected. Captured ants, conserved in alcohol (70%), were identified and counted in the laboratory at the species level, when possible, or at genus level. Only numerically and behaviourally dominant species (defined as highly aggressive species that usually predomi- nate numerically, occupy large territories, and have mutually exclu- sive distribution patterns at local scales) determined following the criteria defined by Baccaro et al., (2010), were considered in the analysis. Rare species (with occurrence<2.5%) were not considered. Ten species were therefore retained for the analysis: *Solenopsis picea* (Emer, 1896), *Camponotus sericeiventris* (Mayr, 1861), *Solenopsis geminata* (Fabricius, 1804), *Nylanderia steinheili* (Forel, 1893), *Pseudomyrmex simplex* (Smith, F., 1877), *Crematogaster curvispinosa* (Mayr, 1862), *Pheidole* spp. (Westwood, 1839), *Dolichoderus validus (*Kempf, 1959), *Cephalotes multispinosus* (Norton, 1868) and *Cephalotes cristatus* (Emery, 1890). Among these species, a functional group, named CBB antagonist, was constituted, consisting of species considered as CBB predators (*S. picea, N. steinheili, P. simplex, S. geminata* and *Pheidole* spp.) (Armbrecht and Gallego, 2007; Armbrecht and Perfecto, 2003; Bustillo et al., 2002; Gonthier et al., 2013; Larsen and Philpott, 2010; Morris and Perfecto, 2016) or as territorial species (*C. sericeiventris* and *D. validus,* due to their aggressive and colony extension abilities that can lead to exclusion of others species). Based on literature and on the numerical weight of the species, we further decided to split the functional ant predatory group in two groups: group G1 consisting of *Solenopsis* species and Group G2 consisting of the six other antagonistic species. The abundance of the groups per plot was calculated as the mean of the sum of the abundance of the species on the four coffee trees and the central plant over the three sampling campaigns.

2.3 Data analysis

Plots with less than five berries suitable for CBB infestation in April or October 2018 were not considered, leaving 45 plots for the analysis.

The effect of the three farm on the environmental variables were tested against a null model with a chi-square test. A multiple comparison (multcomp package) (Hothorn et al., 2008) using the post hoc Tukey test was then performed to evaluate difference among the three treatments. Correlations between environmental variables were tested using Pearson correlation tests. The same approach was used to test the effect of the farms on global ant-specific richness.

To highlight indirect relationships that could not be explored in simple models and, in particular, considering a variable as both an explanatory and response variable, we performed structural equation modeling (Grace, 2006) by using the piecewiseSEM R package (Lefcheck, 2016). Based on a preliminary analysis of the results and on literature, we defined different hypothetical links involved in CBB regulatory service in coffee AFS. Seven sub-models were constructed to test hypothesized causal relationships (Table 2). According to response variable distributions, the two CBB infestation sub-models were binomial general linear models (GLMs). For G2 abundances we used Poisson GLMS and for CBB adult population, the initial fruit load and G1, we used quasi-GLMs with a Poisson error, which provided an improved fit to over-dispersed count data (Zuur et al., 2009). According to the piecewiseSEM method described in (Lefcheck, 2016), the global path model is considered to represent the data well when the p-value of this chi-squared test is greater than the significance threshold. For each variable response, an R squared (R^2) was provided.

Response variables	Explanatory variables	Hypothesized mechanisms of regulation	References
%SC	FMS[1]+CD[1]+TSA[1]	[1] Microclimate creation	(Lin, 2007; Vaast et al., 2006)
AdCBB	FMS[2]+%SC[3]+CD[4]+TSA[5]	[2] Management	(Damon, 2000; Roth et al., 1994)
Peak CBB	FMS[2]+%SC[3]+CD[4]+ TSA[5]+ IniCBB[6]+AdCBB[6]+ G1[7]+G2[7]	[3] Bottom up (microclimate)	(Mariño et al., 2016; Perfecto and Vandermeer, 1996)
IniCBB	MFS[2]+%SC[3]+CD[4]+TSA[5]+Ini. Fruit[4]+AdCBB[6]+G1[7]+G2[7]	[4] Bottom up (ressource)	(Ribas et al., 2003; Rodríguez et al., 2013)
Ini. Fruit	%SC[1]+FMS[1]+CD[1]+TSA[1]	[5] Bottom up (barrier effect)	(Schroth et al., 2000)
		[6] Pest population dynamic	(Avelino et al., 2012)
G2	FMS[2]+%SC[3]+CD[4,9]+TSA[4,9]	[7] Top down	(Gonthier et al., 2013; Jiménez-Soto et al., 2013)
G1	FMS[2]+%SC[3]+CD[4,9]+TSA[4,9]	[8] Plant growth and phenology	(Rodriguez et al., 2011)
		[9] Bottom up (Habitat)	(Lassau and Hochuli, 2004)

Table 2. Sub-model equation constituting the global path model based on hypotheses from bibliographic reference regarding the relationships between response variables and explanatory variables. %SC: percentage of shade cover; AdCBB: CBB adult population; PeakCBB: CBB infestation at the fruit peak season; IniCBB: CBB infestation at the beginning of the fruiting season; IniFruit: Initial fruit load; G1:Abundance of the G1 group; G2:Abundance of the G2 group; CD: Coffee density; TSA:Tree surface area; FMS: Farm Management strategy

For the damage analysis, we used a multinomial logit model to assess the effect of farm management, ant abundances (G1 and G2), %SC, CBB infestation at the fruit peak season and the presence of CBB adults inside the fruit on the berry damage. Damage with Score 1 was used as reference in the model. We removed non-significant effect parameters in a backward, stepwise process using the likelihood-ratio test (LRT). The selection procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). All statistical analyses were performed with R Version 3.5.0 (R Development Core Team 2018).

3 Results

3.1 Environmental variables at plot scale

Three environmental variables evaluated at plot scale (%SC, tree species richness and maximal temperature) varied significantly according to farm management (respectively, $F(df=2)=23.8$, $p<0.01$; $F(df=2)=4.19$, $p=0.02$; $F(df=2)=3.6$, $p=0.03$). The %SC and tree species richness decreased significantly from conventional farm to organic farm (Table 1). The %SC fluctuated between 49.05 and 85.49% in the three sites, with a mean of 79.98% (+/- 0.93%) in the conventional farm, 71.97% (+/- 1.55%) in the integrated farm and 65.83% (+/- 1.68%) in the organic farm. Tree species richness was positively correlated with the %SC ($R=0.41$, $p<0.01$) whereas maximal temperature was negatively correlated with the %SCR=-0.38, $p=0.01$). We decided to keep the %SC within the complete model, taking into account the effect of farm. CD (coffee density) and TSA (tree surface area) were not correlated neither with the farm nor with the %SC. CD ranged from 1.23 to 2.28 plants per m^2 (97 to 179 plants per plot of 153 m^2 each). The mean CD within plots were 133.65 (+/- 5.21), 136.78 (+/- 8.82) and 132.75 (+/-5.28) per plot, respectively, in the conventional, integrated and organic farms. TSA ranged from 0.02 m^2 to 2.31 m^2 per plot, with on average 0.37 (+/-0.11 m^2) in the conventional farm, 0.26 (+/-0.06 m^2) in the integrated farm and 0.19 (+/- 0.03 m^2) in the organic farm.

3.2 Pest populations at plot scale

Mean CBB infestations per plot were similar at the beginning and at the peak of the fruiting season for all the farms; 6.89% (+/-1.34%) and 6.20% (+/- 0.88%) ($t=0.43$, $df=76.01$, $p= 0.67$), respectively. Difference of CBB infestation rate between the farms will be described in the section 3.4 of the results. Within the farms, IniCBB was not different from PeakCBB. On the other hand, the mean number of total sampled fruits per plot was higher during the peak

(106.04 +/- 5.84) than at the beginning of the season (29.44 +/- 3.31) (t=-10.47, df=69.5, p<0.0001). AdCBB that were captured varied from 1 (organic farm) to 46 (conventional farm) per trap for six days of capture, with a mean of 17.66 (+/- 2.48 individuals) in the conventional farm, 9.99 (+/- 1.74) in the organic farm and 10.85 (+/- 1.21) in the integrated farm.

3.3 Ant communities at plot scale

Over the three sampling campaigns, 78 species were collected with the two sampling methods and were identified (Appendix 1). The total abundance of these species was highly unbalanced: 49 out of 78 species showed a total abundance below 10 individuals. Ant specific richness ranged from 1 to 17 species within plot. The mean specific richness was significantly higher in conventional farm (10.55±0.80) and integrated farm (10.33±0.85) than organic farm (5.65±0.46) (respectively p<0.0001 and p<0.002, Tukey's test). The mean specific richness was not significantly different between the integrated and conventional farms (p=0.98, Tukey's test).

Among the eight species of the ant predatory group, *Solenopsis* species (G1) were largely overrepresented in the plots. *Solenopsis picea* was the most abundant and the most common (Table 3). It was found in all the plots at least one time and was present on more than 49% of the sampled coffee trees. *Solenopsis geminata* was also numerically (third most abundant species) and behaviourally dominant, with a mean global dominance of 27.8% of the sampled trees; it was not found dominant on any trees of the organic farm though it was present on that farm. In the G2 group, the *P. simplex, Pheidole* spp. and *D. validus* ants had the largest occurrence. *Pheidole* spp. had a mean occurrence of 10.9% on all the sampled trees and was the second most abundant genera (Table 3).

Species	Global occurrence (%)	Farm occurrence (%)			Global dominance (%)	Farm dominance (%)			Total abund.
		Integ.	Orga.	Conv.		Integ.	Orga.	Conv.	
S. picea	49.1	35.8	58.1	47.3	13.6	7.5	15.8	13.4	3253

S. geminata	2.6	3.4	0.7	3.9	27.8	40	0	27.3	383
Pheidole spp.	10.9	16.2	2.6	16.3	14.3	8.3	0	19.6	934
C. sericeiventris	2.8	7.4	1.8	1.4	0	0	0	0	26
N. steinheilli	5.4	3.4	2.9	8.8	0	0	0	0	134
P. simplex	9.2	25.7	6.2	3.5	0	0	0	0	90
C. curvispinosa	2.6	4.7	0	3.9	0	0	0	0	25
D. validus	8.5	2.7	6.6	13.4	0	0	0	0	172

Table 3. Mean global and farm occurrence, mean global and farm dominance, and total abundance of the eight ant species of the ants predatory group in the plots. A species was considered as dominant on a sampled tree if its abundance (1) was higher than 20 while it was the only species present on the tree or (2) if its abundance was twice as high as the second more important taxon on a tree on which total abundance was higher than 20.

3.4 CBB regulation in the triple interaction network

Our global path model represented the data well (Fisher's C=10.20, df=12, $\chi 2$ test p=0.60) and 16 out of 42 links tested were significant. Pathway coefficients and significance levels are presented in Appendix 2. The different sub models of the SEM that explained AdCBB, IniCBB, PeakCBB, IniFruit, %SC, G1 and G2 explained a globally important percentage of the variance with R^2 of the sub-models, varying from 0.18 to 0.54 (ApendixC) and suggesting a good fit between the built model and observed data. The significant causal relationships between the environmental variables, the predators and the CBB populations are summarized in Fig.1. The %SC was significantly influenced by the farm management. It was significantly lower in the organic and integrated farms in comparison with the conventional farm. This environmental variable significantly reduced IniFruit in the plots, which was positively correlated with IniCBB. AdCBB in the plots was also negatively correlated to the %SC, while IniCBB was positively correlated to the %SC. Both organic and integrated farms reduced AdCBB in comparison with the conventional farm, and the integrated farm had less IniCBB

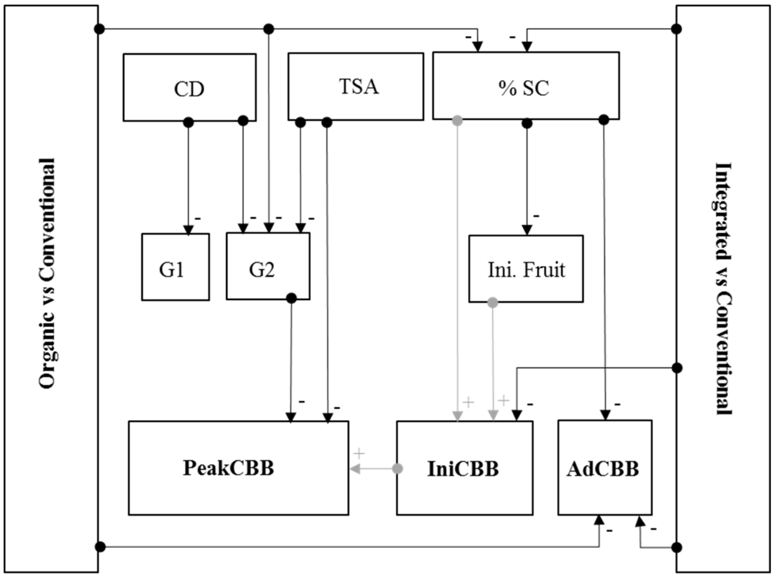

Fig.1. Representative summary of the global pathway model results showing the effects of farm management and plot characteristics on CBB population and on the abundance of two groups of predatory ants and on biotic interactions between these two communities. Black and grey arrows represent significant ($p<0.05$) positive and negative relationships, respectively.

than the conventional farm. The ant group G2 was less abundant in the organic farm compared with the conventional farm. It was also negatively related with TSA within the plot. Both predator groups G1 and G2 were negatively correlated with CD. The maximal percentage of bored fruits obtained in fruit peak season was positively correlated to IniCBB, but it was negatively related to the associated tree surface area and to the abundance of the G2 group.

3.5 Relation to agronomical indicators

The proportion of damaged cherries (proportion between score 0 and score 1 and proportion between score 2 and score 1) sampled in October 2018, at the plot level, was significantly related to the farm management ($\chi2$ (df=4)=77.55, $p<0.001$), to %SC ($\chi2$ (df=**2**)=13.27, $p<0.01$), to peak CBB ($\chi2$ (df=2)=8.86, p= 0.01) and to the abundance of the G1 groups ($\chi2$ (df=2)=16.62, $p<0.001$). For the three farms, mean % of cherries with score 1 was 83.36% (+/- 0.91), whereas mean % of cherries with score 0 and 2 was lower (respectively, 8.84% +/- 0.63

and 7.69% +/- 0.62). The proportions of cherries with no damage and with score 2 were significantly higher for the integrated farm in comparison with the conventional and organic

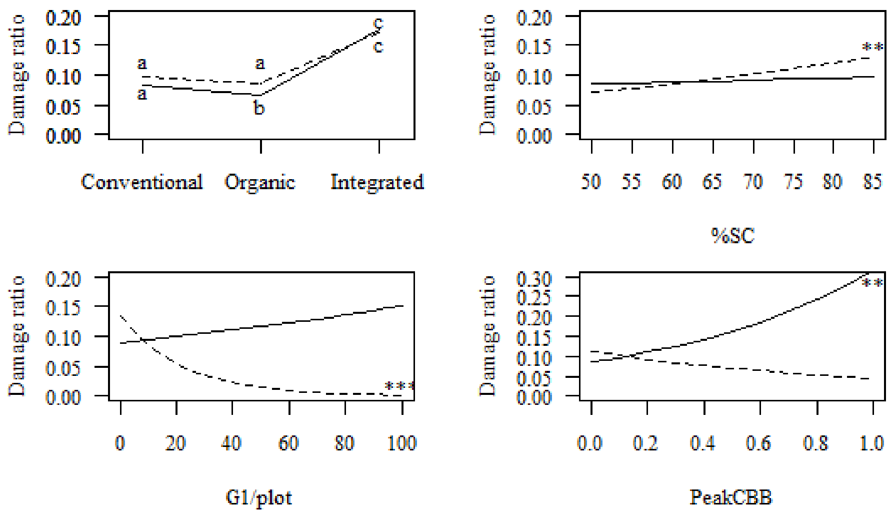

Fig. 2: Evolution of damage ratio (dash line: Score0 / Score1; plain line: Score2 / Score1) considering farm management, %SC, abundance of G1 and PeakCBB per plot. Different letters refer to difference among farm management for the two damage ratio (Fisher test). Asterisks refer to significant effect of the predictive variables on damage ratio (** p<0.01; *** p<0.001)

farms (Fig. 2). On the other hand, only the proportion of cherries with score 2 was significantly lower for the organic farm in comparison with the conventional farm (Fig. 2). The proportion of cherries with no damage significantly increased with higher %SC (p=0.001; estimate=0.03)

and decreased with higher abundance of G1 (p<0.001; estimate=-0.04). Finally, the proportion of cherries with high damage (score 2) was positively related to PeakCBB.

4 Discussion

We aimed to assess a regulating service in complex AFS by adopting a holistic approach. To do so, we considered the tripartite network (CBB–ants–environment) of coffee-based AFS.

4.1 Bottom-up effects of environment on CBB infestation

We hypothesized that environmental variables would have negative, bottom-up effects on CBB infestation based on the resource dilution hypothesis (Ratnadass et al., 2012). In our model, we did not find any evidence of this effect. By contrast, we found a significant negative effect of TSA on PeakCBB, which is more in favor of a barrier effect for CBB infestation. CBB dispersal occurs mainly near infested berries, but it also occurs over slightly longer distances with air stream (Damon, 2000). Tree stratum could prevent displacement of CBB from tree to tree (Staver et al., 2001). On the other hand, we found that %SC, which was negatively related to maximal temperature and positively related to tree species richness, was a key environmental variable. In fact, %SC had a negative influence on IniFruit, which in turn was positively correlated to IniCBB. Shade is known to influence CBB populations through its effect on the coffee plant, particularly on its phenology (Staver et al., 2001), which is a key factor explaining the growth of CBB populations (Rodríguez et al., 2011). We also found a direct positive effect of %SC on IniCBB and a negative effect on AdCBB. Shaded systems have often been reported to favour CBB infestations (Bosselmann et al., 2009; Mariño et al., 2016; Teodoro et al., 2008) in comparison with full sun systems, even though some studies failed to find any effect (Soto-Pinto et al., 2002). Shade tends to buffer temperatures and to maintain humidity close to the optimum for CBB survival (Damon, 2000). We also found that %SC has a negative effect on damage intensity. This result is comparable with those of Mariño et al. (2016), who observed that even if the infestation rate is higher under shade, the number of individuals inside the fruit is lower and lower damage can be expected.

4.2 Bottom-up effects of environment on ants

We hypothesized that environmental variables would have (positive) bottom-up effects on the abundance of predatory ants (Ribas et al., 2003). We found that CD was correlated with a lower abundance of both the G1 and G2 groups of ants. This negative effect could be an indirect effect of coffee age in the plots. In our study, higher coffee density is observed in youngest systems (personal communication) which could potentially affect soil macrofaunal biodiversity. In fact, in rubber systems, older plantations harboured have highest microbial and macrofaunal biomass (Peerawat et al. 2018). But more studies are needed to confirm this hypothesis. Most of the predatory ants considered in our study, whether in the G1 group (Solenopsis species) or in the G2 group (*N. steinheili* and some *Pheidole spp.*), are ground-foraging and -nesting (Antweb 2019). Only *Dolichoderus validus* is known to be strictly arboreal. The groups of ants we studied was probably more positively influenced by the composition of the ground stratum (not considered in our study) than by tree composition. For instance, Poeydebat et al. (2016) found a direct effect of the low-stratum plant richness on the activity-abundance of omnivorous ants in AFS in Costa Rica. Indeed, considering that we worked with a functional group that is structured by strong relationships and by different niche preferences, the overall effect of environmental conditions on these groups could be hard to summarize. Some environmental conditions, such as shade, for example, could have a null overall net effect as it could favor one species and disadvantage the other. Some species such as *P. simplex* have specific niche requirements (twig nest ants) that were not considered here.

4.3 Top-down effects of ants on CBB infestation

We hypothesized that predatory ants would have a negative top-down effect on the CBB infestation (Jiménez-Soto et al., 2013). We found that the peak of infestation was lower when the abundance of ants of the G2 group was higher. This result suggests that some species of this G2 group are preying on free CBB adults or preventing them from boring coffee berries. Ants of the *Pseudomyrmex* genus, including *P. simplex* (G2 group), have been found to feed on free and berry-embedded CBB in laboratory experiments (Gonthier et al., 2013; Larsen and Philpott, 2010), while *Pheidole synanthropica* ants have been observed predating on CBB during a prey-sentinel experiment. Ants may also deter or actively prevent CBB access to berries (Jiménez-Soto et al., 2013). We did not find a top-down effect of G1 on the peak of infestation and we also showed that the proportion of bored fruit without damage decreased when G1 abundance increased. The role of these Solenopsis species in CBB biological regulation is controversial since some authors found a significant impact of *S. picea* on CBB infestation (Armbrecht and Gallego, 2007; Morris and Perfecto, 2016) and others did not find anything (Gonthier et al., 2013). *Solenopsis geminata,* through aggressive behaviour, can prevent CBB removal by suppressing other ant species on coffee trees that are CBB predators (Trible and Carroll, 2014). Our results reinforce the idea that *S. picea* and *S. geminata* are probably not predators of CBB. Studying top-down effects of the ant community on pest suppression in the field is relevant and more realistic, but it is also a delicate task requiring a good knowledge of ant ecology.

4.4 Effect of management on the tripartite network

Organic and integrated farms have a significant negative effect on CBB populations at the beginning of the fruiting season (IniCBB and AdCBB) in comparison with conventional farms. In those two farms, farmers used to practice postharvest sanitation, which is known to be very effective in decreasing CBB populations (Aristizabal et al., 2016; Avelino et al., 2012; Jaramillo et al., 2006; Johnson et al., 2019). The farm management also had an effect on %SC per plot, with the highest percentage encountered in the conventional farm, which was also the most diversified in terms of plant diversity and richness. The %SC can counterbalance the effect of the CBB regulation strategy. If shade is known to favor CBB by providing better microclimatic conditions for completing the CBB life cycle, it also provides better conditions for *Beauveria bassiana* parasitism and reduces CBB infestation when this entomopathogenous fungus is applied (Aristizabal et al., 2016; Vega et al., 2015), which is the case for the integrated farm. However, further investigation is needed to explore the efficiency of the local strains of *B. bassiana* used by the farmers under shaded conditions. Farm management also had an effect on the abundance of G2, which was lower in the organic farm in comparison with the more diversified conventional farm, in which chemical insecticides used to be used and herbicides are used. Negative effects of intensive managements on ants is well described (Roth et al., 1994), but could have been masked in our study by different levels of biodiversity between sampling sites. Abundance of predatory ants is more likely influenced by tree global diversity within AFS than by tree local diversity. Our results also confirmed that higher infestation rates at the peak season is positively correlated with higher damage (Aristizabal et al., 2016). In fact, all the strategies that can reduce CBB infestation rates could be able to reduce overall damage and losses caused by the pests.

Here we present a method to study the combine effects of environmental conditions and non-specific natural enemies of CBB. Another step to improve IPM in this area, could be to include more specific natural enemies if they are present in the area (*i.e.,* parasitoids and specific predators of CBB in remnant fruits like flat bark bettle (Follet et al., 2016)) in the analysis to provide more accurate recommendations to farmers in term of CBB management strategies. In fact, it is of great importance to understand how plant diversity within the systems can modify natural enemies dynamics and also what is the effect of entomopathogen fungus (i.e., *B. bassiana*) on this community.

Finally, the statistical method we used (structural equation) to analyse the data is very powerful to investigate complex interactions within complex system like the ones we studied. It is also very sensitive to available data and to the conceptual model that we built.

In conclusion, our study suggests that a combination of bottom-up and top-down effects (via significant ants' effect) emerging from farm management (shade, plant diversity, pest and disease regulation) helped to maintain a low level of CBB infestation and damage within the AFS. Both global (farm scale) and local (plot scale) diversity should be considered to explain CBB infestation and damage and abundance of predatory ants. Our results confirm that the best way to regulation CBB is to practice sanitary harvest at the end of the harvesting season and to conserve a high level of tree diversity within the farm to maintain good predator diversity and to regulate shade intensity.

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Appendix

Species	Number of occurrence
Solenopsis picea	49
Pseudomyrmex simplex	29
Pheidole spp	26
Paratrechina steinheili	24
Dolichoderus validus	21
Solenopsis geminata	14
Cephalotes multispinosus	13
Camponotus sericeiventris	12
Pseudomyrex oki	11
Camponotus brettesi	10
Paratrechina longicornis	10
Crematogaster curvispinosa	9
Paratrechina JTL 014	9
Pseudomyrmex cf gracilis	8
Azteca sp	7
Cephalotes basalis	7
Camponotus senex	7
Simopelta sp	6
Cephalotes cristiatus	6
Nesomyrmex echinatinodis	6
Camponotus sp	6
Crematogaster sp	6
Paratrechina JTL 001	5
Camponotus excisus	5
Tapinoma ramulorum	4
Camponotus JTL 027	4
Camponotus cuneidorsus	4
Pseudomyrmex tenuissimus	4
Procryptocerus kempfi	4
Procryptocerus belti	4
Paratrechina JTL 007	4
Crematogaster monteverdensis	4
Crematogaster stolli	3
Brachymyrmex longicornis	3
Crematogaster sumichrasti	3
Cephalotes minutus	3
Cephalotes cordiventris	3
Camponotus JTL 016	3
Camponotus fastigatus	3
Camponotus planatus	3
Paratrechina caeciliae	3
Crematogaster sotobosque	3
Pseudomyrmex subtilissimus	3
Platythyrea punctata	3

Atta cephalotes	2
Camponotus JTL 045	2
Camponotus sanctaefidei	2
Tapinoma litorale	2
Solenopsis sp	2
Camponotus novogranadensis	2
Cephalotes peruvienses	2
Cephalotes scutulatus	2
Cardiocondyla minutior	2
Gnamptogenys.sulcata	1
Pachycondyla foetida	1
Simopelta JTL 004	1
Nessomyrmex JTL 008	1
Crematogaster distans	1
Pachycondyla laevigata	1
Pachycondyla crenata	1
Camponotus striatus	1
Brachymyrmex heeri	1
Crematogaster tenuicula	1
Camponotus JTl 056	1
Camponotus JTL 043	1
Camponotus JTL 005	1
Camponotus claviscapus	1
Tapinoma melanocephalum	1
Nesomyrmex asper	1
Eciton hamatum	1
Pseudomyrmex cf termitarius	1
Gnamptogenys alfaroi	1
Cephalotes stulifer	1
Crematogaster nigropilosa	1
Forelius sp	1
Cyphomrmex sp	1
Ectatomma ruidum	1
Brachymrmex sp	1

AppendixA: Species sampled over the three periods and their occurrence at plot level (number of times the species was sampled from the 147 sampling done over the three periods)

Response variables	Explanatory variables	Predictor (SE)	P-value	
% shade cover	Organic vs conventional	-0.14 (0.02)	**7.67e-08**	***
R²m=0.54	Integrated vs conventional	-0.08 (0.02)	**0.0043**	**
	Coffee density	-0.05 (0.06)	0.3926	
	Tree surface area	0 (0.03)	0.8782	
Adult population (AdCBB)	Organic vs conventional	-1.05 (0.31)	**0.0019**	**
R²m=0.32	Integrated vs conventional	-0.73 (0.28)	**0.0126**	*
	% shade cover	-3.72 (1.54)	**0.0209**	*
	Tree surface area	0.27 (0.21)	0.2098	
	Coffee density	-0.01 (0.59)	0.9885	
CBB Peak Infestation (PeakCBB)	CBB initial infestation	4.37 (0.65)	**1.62e-11**	***
R²m=0.29	Tree surface area	-1.87 (0.45)	**3.32e-05**	**
	G2 abundance	-0.02 (0.01)	**0.0280**	**
	Coffee density	-0.56 (0.45)	0.2137	
	Adult population	-0.01 (0.01)	0.4266	
	Organic vs conventional	0.18 (0.25)	0.4768	
	G1 abundance	0.00 (0.00)	0.5106	
	% shade cover	0.52 (1.21)	0.6681	
	Integrated vs conventional	-0.01 (0.24)	0.9775	
CBB Initial Infestation (IniCBB)	Initial fruit load	0.02 (0)	**0.0002**	***
R²m=0.32	% shade cover	5.46 (2.00)	**0.0058**	**
	Integrated vs conventional	-0.84 (0.36)	**0.0209**	*
	Coffee density	-1.50 (0.97)	0.1222	
	Organic vs conventional	-0.52 (0.44)	0.2404	
	G2 abundance	0.00 (0.01)	0.5778	
	Adult population	0 (0.02)	0.7439	
	G1 abundance	0 (0.02)	0.7691	
	Tree surface area	0 (0.39)	0.9901	
Initial Fruit Load	% shade cover	-5.30 (1.49)	**0.0010**	**
(IniFruit)	Organic vs conventional	-0.47 (0.34)	0.1743	
R²m=0.39	Tree surface area	-0.52 (0.48)	0.2822	
	Integrated vs conventional	0.17 (0.29)	0.5472	
	Coffee density	0.30 (0.63)	0.6388	
G2 Abundance	Organic vs conventional	-1.95 (0.45)	**1.10e-07**	***
R²m=0.31	Coffee density	-2.13 (0.69)	**0.0021**	***
	Tree surface area	-0.99 (0.46)	**0.0326**	*
	Integrated vs conventional	-0.26 (0.29)	0.3847	
	% shade cover	-1.12 (2.26)	0.6214	
G1 Abundance	Coffee density	-2.02 (0.90	**0.0304**	*
R²m=0.18	Organic vs conventional	0.36 (0.44)	0.4094	
	% shade cover	1.51 (2.37)	0.5277	
	Tree surface area	0.10 (0.33)	0.7685	
	Integrated vs conventional	-0.01 (0.43)	0.9803	

Appendix 2: Pathway coefficient estimates and p-value from the SEM with G1 abundance, G2 abundance, CBB initial infestation, CBB peak infestation, adult population, initial fruit load, fruit load before harvesting and % shade cover as response variables. $R^2{}_m$ of each selected model are shown under each response variable name.