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Assessing the joint effects of landscape, farm features and crop management practices on berry damage in coffee plantations

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A R T I C L E I N F O

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A B S T R A C T

Coffee berry borer (CBB) (*Hypothenemus hampei*; Coleoptera: Curculionidae: Scolytinae) is a major insect pest affecting coffee cultivation that causes large economic losses worldwide. Characteristics related to its life cycle makes it very difficult to control. Usually, CBB control measures are carried out at plot scale, with almost no actions taken at wider landscape scales. It is unclear how plot level control strategies and landscape factors act alone or in combination to influence CBB infestation levels. We evaluated the joint effects of crop management at the plot level, of farm features, and of landscape structure at different spatial scales on CBB infestation in 50 Costa Rican coffee farms. On five plants in each farm, we estimated the maximum number of infested berries during the fruiting period. We measured three separate groups of variables related to plot management practices, farm features and landscape structure. To assess their single and joint contributions, their relative importance and the effects of these variables on the number of infested berries we used the variance partitioning approach of the RandomForest algorithm. When evaluating the groups of factors separately, we found that crop management explained 35% of the variability of number of infested berries, farm features 42% and landscape structure 27%. The joint contribution of all three groups of variables explained 48% of variability of the number of infested berries. However, when we assessed the single contributions of each set of variables, i.e., when controlling the other two set of variables, we found that farm features explained 17% of the variance of the number of infested berries, landscape structure 6% and crop management practices only 3%. The larger amount of the variance explained by the joint effect of crop management practices, farm features, and landscape structure suggests that to develop a pest management strategy at a local scale it is important to consider the effect of both local and landscape factors affecting pest abundance. The integrated CBB management plan should consider influences at multiple spatial scales and a coordinated action among farmers that share the same landscape would be beneficial.

1. Introduction

On-farm practices, as well as landscape composition and configuration, significantly affect arthropod diversity and abundance (Bianchi et al., 2006; Clough et al., 2007; Attwood et al., 2008; Chaplin-Kramer et al., 2011; Flores-Gutierrez et al., 2020). Intensively managed agro-ecosystems, such as monocultures with frequent pesticide applications, have reduced overall arthropod diversity (Attwood et al., 2008). Landscape composition and configuration can promote pest control through the conservation of pests' natural enemies (Milligan et al., 2016; Librán-Embid et al., 2017; Lindell et al., 2018; Martin et al., 2019; Haan et al., 2020). Natural enemy populations can be reduced by homogeneous landscapes with low percentages of natural cover, which might be associated with availability of food resources, nesting locations, or

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refuges, all of which are frequently more abundant in heterogeneous landscapes (Chaplin-Kramer et al., 2011; Karp et al., 2018; Martin et al., 2019; Flores-Gutierrez et al., 2020).

Farm management and the life histories of individual pests and their enemies can modulate landscape effects (Rusch et al., 2013; Karp et al., 2018; Djoudi et al., 2018). Landscape composition and configuration might directly affect a pest's population dynamics by facilitating or obstructing their movement and thus changing the pest́s foraging behavior (Bhar and Fahrig, 1998; O'Rourke and Petersen, 2017). Multiscale approaches are important to understand population dynamics and trophic interactions. Understanding how these interactions contribute to natural pest control can help shift pest management strategies from a local process that is repeated many times within a cropping season, to a more holistic approach that considers multiple factors and scales for action (plot, farm, landscape) (Rusch et al., 2011; Salliou and Barnaud, 2017; Qiu, 2019).

In this study, we develop a multiscale approach to study pest damage using as our test case the coffee berry borer (CBB), *Hypothenemus hampei* (Coleoptera: Curculionidae), the most important coffee insect pest in the world. The coffee berry borer is present across all coffee growing regions of the world, with records of its presence up to 1500 m elevation (Agegnehu et al., 2015; Jonsson et al., 2015; Asfaw, 2019). Inadequate management of CBB infestations has caused major economic losses across the globe due to the pest's direct impacts on coffee yield and quality (Baker et al., 1992; Damon, 2000; Chain-Guadarrama et al., 2019). Its range is limited by its thermal tolerance, with an optimal development thermal range between 15 and 27 °C, and a maximum temperature tolerance around 32 °C (Jaramillo et al., 2010; Azrag et al., 2020). Larval development occurs exclusively within the coffee bean. Female flight is mainly responsible for the species' spread when adults move to colonize surrounding coffee resources. These biological characteristics make CBB difficult to control (Damon, 2000).

Integrated Pest Management (IPM) programs for control of CBB have been proposed that would combine cultural, biological, chemical control, and post-harvest sanitation practices (Aristizábal et al., 2016). Development of effective CBB IPM programs requires detailed knowledge of the population dynamics of the target pest and its natural enemies. Over the last 30 years, CBB population dynamics have been intensively studied due to the severity of the economic losses CBB causes to small and medium size coffee farmers worldwide (Jha et al., 2011). However, most studies on CBB ecology and its control have focused on assessing infestations and the effects of management strategies at the plot level (Rodríguez et al., 2013; Aristizábal et al., 2016; Mariño et al., 2016; Roman-Ruiz et al., 2017; Johnson et al., 2020; Bagny Beilhe et al., 2020). Additional research has focused on understanding the contribution of natural enemies in controlling CBB populations to inform development of conservation biocontrol strategies (Perfecto et al., 2004; Armbrecht and Gallego, 2007; Kellermann et al., 2008; Martínez-Salinas et al., 2016; Morris and Perfecto, 2016). However, many of these strategies have been largely based on parasitoid releases (Rodríguez et al., 2017) or the application of entomopathogenic fungi (Bustillo et al., 1999). More recently, studies have focused on understanding the effects of the surrounding landscape's composition on CBB control, focusing mainly on a landscape's positive effects on boosting natural enemy populations (Kellermann et al., 2008; Karp et al., 2013; Boesing et al., 2017; Aristizábal and Metzger, 2019; Chain-Guadarrama et al., 2019; Escobar-Ramírez et al., 2019).

For instance, in Southeast Brazil, Aristizábal and Metzger (2019) reported that incidence of infested coffee berries increased as the distance between sun coffee plantations and forest patches increased. Karp et al. (2013) found that percentage of on-farm forest cover was a significant predictor of the rate of removal of adult CBB females by birds, with higher forest cover being associated with higher pest control. The presence of forests around coffee plantations could affect CBB numbers either by enhancing predation rates on CBB by natural enemies or by limiting dispersal and colonization of surrounding coffee plantations by CBB adults. Studies on direct effect of landscape context on CBB life cycle, dispersion and incidence are scarce but see Avelino et al. (2012), Roman-Ruiz et al. (2017) and Mosomtai et al. (2021). In coffee plantations in Colombia, Castaño et al. (2005) found that CBB adults tend to disperse up to 30 m and colonize nearby coffee plantations. In Costa Rica, Avelino et al. (2012) found that forest cover acted as a dispersal barrier, such that CBB infestation was less intense in coffee plantations surrounded by high forest cover.

Coffee growing and pest control are affected by changes environmental factors that operate at local and landscape scales and which influence CBB population dynamics. However, these scale-dependent interactions remain mostly unexplored despite their importance for coffee IPM. It is unclear how these factors act alone or in combination to moderate CBB infestation levels. Therefore, the aim of this study was to assess the effects of (1) crop management practices implemented at the plot scale (i.e., CBB control actions, pruning), (2) environmental variables believed to operate at the plot scale (i.e., degree of shade, coffee density) and (3) factors that act at landscape scale (i.e., factors related to the structure of the surrounding landscape) on CBB infestation levels. Considering an estimated average CBB dispersal range (ca 140 m, Olivas et al., 2011), we expected that factors occurring at the plot scale would have the greater effect on the CBB infestation rate. We also expected that factors favoring host plant availability, a location with a suitable climate for CBB development, and vegetation factors facilitating CBB dispersion at both the plot and landscape scales would increase the incidence of CBB infestations.

In the field of ecology, variance partition approaches have been developed to assess the relative importance of multiple factors explaining beta diversity or variation in species abundance. Such approaches contribute to diversity conservation strategies, as well as to the understanding of patterns of organization among organisms through community assembly theories. Different modeling strategies such as general linear and generalized mixed (variance components) models and multivariate techniques (e.g., redundancy analysis, partial mantel tests) are useful tools to partition the total variance of a response variable (uni or multivariate) into multiple explanatory factors (i.e., environmental or biological), separating the unique and share effects of measured factors (Chevan and Sutherland, 1991; Legendre and Legendre, 1998; Walsh and MacNally, 2007; Legendre, 2008; Olea et al., 2010).

We used a variance partitioning approach to i) investigate the effect of unique and joint contributions of crop management practices, plantation characteristics, and landscape structure on the number of infested berries; ii) assess the relative importance of these factors on the number of infested berries, and iii) estimate the type of effect of the different factors occurring at the different scales on the variation of the number of infested berries.

2. Material and methods

2.1. Study area

This study was performed in 2009, within the limits of the Volcánica Central Talamanca Biological Corridor (Lambert 553500–599500 W y 190900–224200 N), located in the Cartago province of Costa Rica, in the Turrialba, Jiménez, Paraíso and Alvarado counties (Fig. 1). Annual average temperature in the study area varies between 24 and 29 °C, with an average relative humidity of 85% and an annual precipitation of 2600 mm (Brenes, 2009). The biological corridor comprises 114,485.22 ha, of which 51% is in forest, 24% in pastures, 4% in sugar cane, and 8% used for coffee cultivation (Brenes, 2009). Coffee (*Coffea arabica* L.) (Catuai and Caturra varieties) is mainly grown in coffee agroforestry systems, in which poró (*Erytrina poepigiana* Walp.) and laurel (*Cordia alliodora* Ruiz & Pav.) are the predominant shade trees in the coffee plantations. Harvest occurs between July and December, peaking typically around November. A variety of management types are used in the region, from conventional management, certified organic, and other

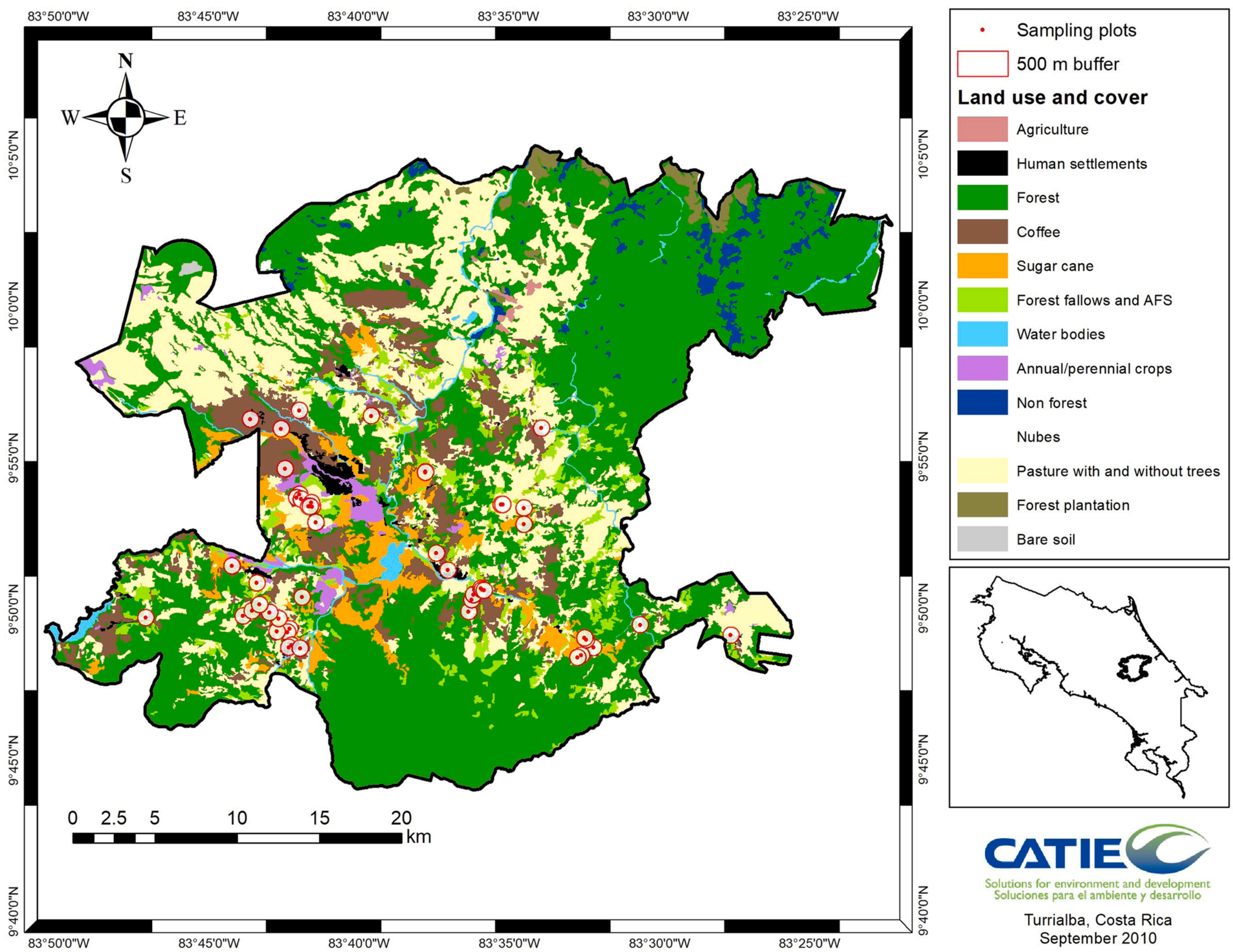

Fig. 1. Distribution of sample farms in the study area. Buffers represents the maximum scale at which landscape metrics were estimated (500 m radius).

certification programs, including the Nespresso AAA sustainable quality program, the Rainforest Alliance, Utz, and Starbuck`s (CAFNET Project, 2009).

2.2. Site selection

The coffee plantations used as study sites were selected by choosing plantations located in different landscape areas that varied in their landscape complexity (from coffee-dominated landscapes to localities where the coffee plantations were highly fragmented) (Avelino et al., 2012). Fifty coffee plantations were selected along a gradient from 613 to 1259 m.a.s.l., with different landscape structure and with different farm management (see description below). Inclusion was also based on farmers' willingness to collaborate with the study and allow access to their farms throughout the year. At each farm site, a plot (average size of 217 m^2) was chosen that was comprised of eight rows of 15 coffee bushes each.

2.3. Characterization of farm features

In the demarcated plots on each farm, we estimated the density of the coffee plants per ha from measurements of the distances between rows and between plants within rows. The height of the coffee trees was estimated at five plants distributed in the form of a cross. In the selected plants, the number of productive nodes per plant was estimate; we counted the number of fruiting nodes present on all productive branches that contained at least 20 fruiting nodes. To characterize the shade conditions on each farm (for the selected plot), we categorized farm plots into four shade groups: (1) shade of legumes tree only, (2) shade of legumes trees and other trees species, (3) shade of bananas (Musaceae) and (4) the absence of leguminous trees or Musaceae (this type also includes plots with lack any shade). The percentage of shade cover was measured with a spherical densitometer twice, one measure taking in May and another one in September based on the time when shade trees were pruned. For each selected coffee plant, four measurements with the spherical densitometer were made cardinal direction. To characterize the degree of shade in the plot, we averaged the measured values. Elevation in meters above sea level (m.a.s.l.) was recorded using a GPS (Table 1). Finally, the age of the coffee system was provided by the farmers (Romero-Gurdián, 2010).

2.4. Estimation of landscape metrics

A land use map was obtained from the photointerpretation of a mosaic of one-meter resolution aerial photographs taken in 2005. The classification process was supported by validation in the field performed in a 500 m radius surrounding each sampling plot in 2008 (Avelino et al., 2012). The landscape surrounding each sampling plot was characterized within concentric circles (buffer) of different sizes (100, 150, 250, 300, 350, 400, 450 and 500 m radius) that represent landscapes of different proximity to the study plot (Thies and Tscharntke, 1999; Steffan-Dewenter et al., 2002; Avelino et al., 2012). In each landscape circle, the percentages of area covered by coffee, forest, sugar, cane, or pastures were estimated. Two other landscapes indices were calculated:

Table 1
Type of management variables and plots evaluated in each of the farms.

Set of variables	Variable	Type of variable	Type of variable specifies
Farm features	Elevation in meters above sea level (m.a.s.l)	Quantitative	Continuous
	Number of young leaves	Quantitative	Discrete
	Age of the coffee system	Quantitative	Discrete
	Number of fruiting nodes	Quantitative	Continuous
	Plant height	Quantitative	Continuous
	Variety	Categorical	Nominal
	Distance between coffee rows	Quantitative	Continuous
	Distance between coffee plants	Quantitative	Continuous
	Density of coffee plants	Quantitative	Continuous
	% Shade	Quantitative	Continuous
	Shade type	Categorical	Nominal
Crop management practices	Pruning of shade trees	Quantitative	Frequency
	Type of pruning	Categorical	Nominal
	Number of weeding cycles	Quantitative	Frequency
	Chemical insecticide application	Categorical	Binary
	Beauveria bassiana application	Categorical	Binary
	Coffee berry borer traps use	Categorical	Binary
	Remnant infested berries (sanitation harvest)	Quantitative	Discrete

the Shannon Evenness Index (SHEI) and the grain index. The SHEI measures the ratio between the actual Shannon's diversity index and the theoretical maximum of the Shannon Evenness Index (SHEI) and is calculated as follows:

$$SHEI = \frac{-\sum_{i=1}^{m}(P_i * \ln P_i)}{\ln m}$$

where Pi is the proportion of land use in class I, and m the number of land use classes. The index ranges from 0 (when only one patch is present, in this case coffee) to 1 (when the proportions of all classes are equal) (McGarigal and Marks, 1995).

The grain index characterizes the openness of the landscape (measures the degree of aggregation), which in our case was estimated as the distance between centers of land patches classified as coffee. The distances were categorized into four classes (class 1 and 2 represent the shortest distance, and class 3 and 4 the longest distances between coffee cells) which are equidistant between the minimum and maximum image cell distance according to the buffer (Max. distance – Min. distance/4). For each class, all cells are counted (Betbeder et al., 2015). Then the following equation was applied to calculate the landscape grain index:

$$grain \quad index_i = \frac{(C3_i + \quad C4_i)}{(C2_i + C3_i)}$$

where C1, C2, C3, and C4 are the frequency of cells in each of the distance classes for the ith sampling point. The grain index for coffee provides fine-scale information about how the sampling plots are aggregated degree with respect to surrounding coffee area. A high grain value (coarse grain) label implies the existence of an open pattern to the landscapes. The grain index was calculated every 10 m from 50 m of buffer to 100 m of buffer, then every 50 m.

2.5. Characterization of crop farm management

To characterize farmers CBB management we interviewed them about their use or not of traps for CBB, chemical insecticides, application of the entomopathogen *Beauveria bassiana*, the use or not of shade trees pruning and if used, the annual pruning frequency, and the number cycles of cutting of non-crop vegetation (weeding) (Table 1). Another activity, sanitation harvesting, which consists of collecting remnant berries in the plant after harvest, were evaluated by counting the number of remnant berries on the ground below plants and on branches in February 2009 (after the 2008 harvest period). We made the assumption that the higher the number of remnant berries that we collected, the lower the number removed by sanitation harvest would have been. Farmers follow Icafe recommendations to implement CBB traps and B. bassiana application, i.e., 20 traps/ha after harvesting or even during the harvest season, and B bassiana application around 60–80 days after flowering, and up to three times a year in regions such as Turrialba where multiple flowering events occur.

2.6. Estimation of number of CBB-infested berries per plant

Within each plot, five coffee plants were distributed in a cross shape pattern were selected at each sampling period (see below). Plants corresponded to healthy and productive coffee bushes, homogeneous in height and architecture, separated by a distance of 5–15 m between them. On each plant, four branches with berries were selected, choosing one each from four vertical strata within the plant, for a total of 20 branches sampled per plot and a minimum of 200 fruits suitable for CBB infestation per plot. On each sample branch, we counted the number of visibly infested ("bored") coffee berries (ones with a visible hole at the apex of the berry where the adult CBB entered). We then counted the total number of fruiting branches per coffee plant and estimated the total number of infested berries per coffee plant as the ratio (Avelino et al., 2012).

Sampling of the number of CBB-infested berries per plant was done four times between May and November 2009: once at the end of the dry season when mature berries (May), twice during the rainy season (berry maturation period) (July and September), and once at the peak of harvest (November). Given that the phenology of different coffee varieties caused the time of peak harvest to differ among farms, we decided to use the maximum of infested berries per plot as a response variable for statistical analysis in all four sampling periods.

2.7. Data analysis

To assess the relative contribution of landscape metrics, plot characteristics, and management practices on the variable "maximum number of infested berries (as described above), we used a Random Forest algorithm (Breiman, 2001). Random forest is a recursive technique of use of binary trees for classification or regression tasks to obtain precise predictions (Breiman, 2001).

This algorithm is most useful for data sets with high dimensionality and redundancy problems in the explanatory variables since each tree in the forest is trained on a random subset of the total data training set. The approach can capture nonlinear relationships well. This technique allows one to identify the most important variables using a measure of mean decrease in accuracy and the mean decrease in mean square errors.

A recurrent issue in studies where landscape metrics are estimated in nested concentric circles of different size, is a high redundancy in estimated landscape metrics within these landscapes at different scales, which carries collinearity problems between explanatory variables. Although Random Forest is a robust algorithm to deal with collinearity, high redundancy in metrics calculated at different landscape extensions results in changes in the order of the variables' importance each time a model is run. To consistently identify the most important landscape variables from data calculated at different radius sizes, we ran all possible models, combining the extension while maintaining one variable of each estimated metrics in each model. The total number of estimated models was 826,686. The selection of the best model was based in the determination of the pseudo-coefficient (R^2) estimated from mean square error. For each combination, the number of solicited of trees grown was 500, with 100 permutations (Breiman, 2001).

We used a partial regression tree to determine the relative importance of management, plot, and landscape context characteristics on the maximum number of infested berries (Legendre, 2008). Hereafter the term "table of variables" will be used to refer to any of the set of variables corresponding to landscape metrics, plot characteristics, or management practices.

We started by constructing regression trees for each table of variables separately to determine the level of variability in the maximum level of infested berries that was explained by each table of variables, without controlling for any other table of variables. We then, modified the regression trees by considering the explanatory variables contained in two tables of variables (landscape + plot, landscape + management, and plot + management). Using the residuals of these models as the response variable, we separately adjusted the regression trees for each table of variables to determine the unique contribution of each table of variables while controlling for the other two table of variables (partial model; landscape| plot+management, plot| landscape+management and management| landscape+plot). Finally, we constructed a regression model in which we combined all tables of variables (complete model). Using the results of this last model, we assessed the relationship between each explanatory variable and the maximum number of infested berries through partial graphs. In summary, with the results of all models, we were able to determine how much of the variation in the maximum number of infested berries was explained by the joint or unique contribution of each table of variables (Fig. 2).

All models were run using 500 trees and 100 permutations. Moreover, we ran 1000 iterations of each model to estimate the average importance of each variable and the average percentage of variation from all models. Running 1000 iterations ensured the stability of explained variance estimations. Partial graphs were generated based on these 1000 iterations. To avoid the effect of extreme values and normalize the data on infestations, in all models the data on the maximum number of infested berries were transformed to its natural logarithm (1 + Y). All explanatory quantitative variables were scaling and centering. All analyses were performed using the software R 3.6.1 (R Core Team, 2019) and the RandomForest library (Liaw and Wiener, 2002). Graphs were built using the ggplot library (Wickham, 2016).

3. Results

3.1. Characterization of management types, plots, and landscapes

The average maximum number of infested berries per coffee plant was 55 (± 95.13 SD), with a maximum of 533. In five plots, there were no infested berries. Fourteen percent of all farmers interviewed did not prune the shade trees in their coffee plantation, while 72% pruned at least twice each year and 12% did so three times each year. Fourteen percent of farmers applied chemical insecticides on their coffee plants, 28% used *B. bassiana* and 26% used CBB traps. In 15 plots, there were no remnant infested berries, but in the other plots, there were from 1 to 31 left over infested berries per plant. Nearly half (48%) of the farmers weeded their coffee plantations at least twice each year, two farmers did so up to six times, and only one farmer did no weeding.

Plots were distributed in elevations between 613 and 1182 m.a.s.l., with an average elevation of 871 m.a.s.l. Plantation age varied from 3 to 50 years, with an average age of 19. The density of coffee plants varied from 3185 to 9520 plants per hectare, with an average of 5571. The distance between rows was between 1 and 2.16 m, while the distance between plants varied from 0.72 to 1.61 m. The percentage of shade over the plots varied from 0 to 59. Shade was provided most commonly (49%) by species of Musacea (bananas), while leguminous trees in association with other species were used in 30% of the plots, and leguminous trees alone in 17%. Only two plots had no shade cover at all. The number of fruiting nodes varied from 7 to 676 nodes per plant.

The landscape surrounding the study area was mainly composed of coffee plantations, from 65.6% of land area at 100 m to 40.1% at 500 m. The percentage of surrounding land determined as coffee plantation decreased as the radius of the buffer surrounding the plot increased (Table 2) because the percent of the landscape in forest increased at larger spatial scales. The percentage of land in pasture or sugar cane was less sensitive to the size of the radius used outward from the plots to define the landscape. The landscape Shannon evenness index increased with the size landscape radii, indicating that the landscape become more heterogeneous at larger scales. The grain index also greatly increased with landscape size, indicating that when the radii of the concentric circles around plots increased, the coffee landscape became more open

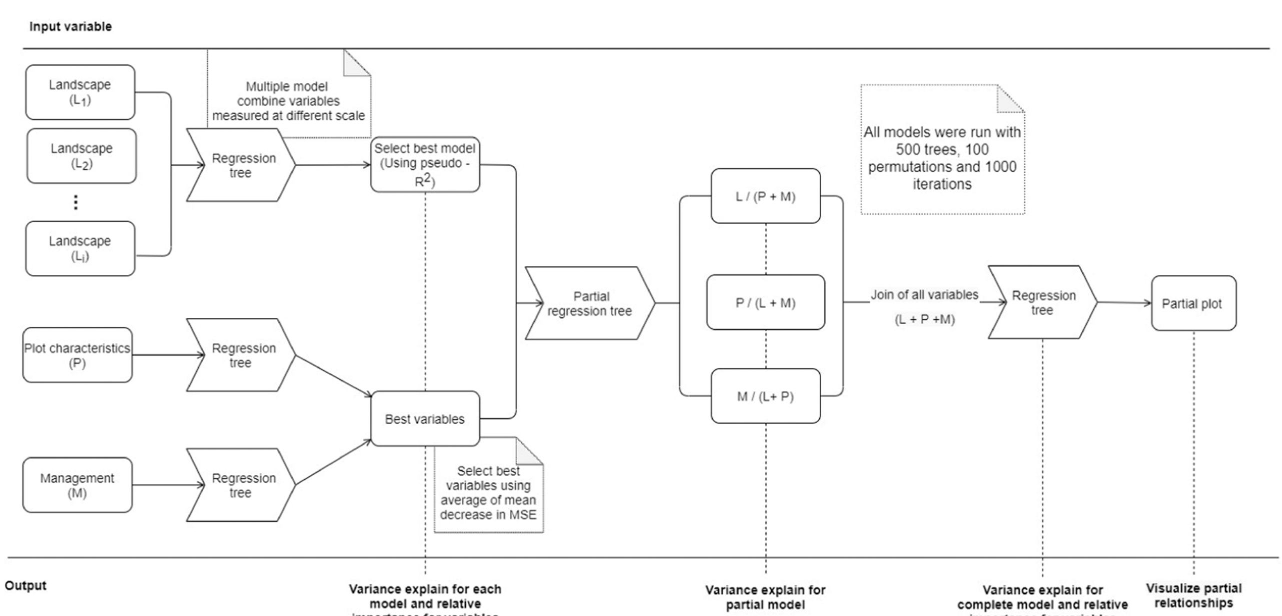

Fig. 2. Workflow of the analysis to assess the relative contribution of all variables (management, plot characteristics and landscape) on maximum number of infested berries using Random Forest algorithm. L1, Li = Its combination of landscape metrics for each model. MSE = Mean Square Error.

Table 2
Mean and standard deviation of each of the landscape metrics calculated at different landscape extensions and used to explain variation in the maximum number of coffee berries infested by coffee berry borer, Hypothenemus hampei.

Buffer (m)	% Coffee	% Forest	% Pasture	% Sugar cane	Evenness index	Grain
50	–	–	–	–	–	0.09 ± 0.21
60	–	–	–	–	–	0.10 ± 0.20
70	–	–	–	–	–	0.11 ± 0.20
80	–	–	–	–	–	0.13 ± 0.20
90	–	–	–	–	–	0.14 ± 0.20
100	65.63 ± 27.57	4.38 ± 10.96	9.11 ± 13.81	16.25 ± 24.65	0.61 ± 0.29	0.16 ± 0.21
150	57.52 ± 29.25	8.99 ± 15.13	10.59 ± 14.00	17.79 ± 25.74	0.61 ± 0.23	0.23 ± 0.23
200	51.60 ± 28.88	13.91 ± 17.03	11.47 ± 13.11	17.94 ± 24.31	0.65 ± 0.21	0.30 ± 0.26
250	47.89 ± 28.45	16.94 ± 17.87	11.69 ± 12.19	18.10 ± 22.68	0.67 ± 0.21	0.35 ± 0.27
300	45.44 ± 28.07	19.34 ± 18.11	11.73 ± 11.59	17.75 ± 20.99	0.67 ± 0.20	0.39 ± 0.27
350	43.63 ± 27.56	21.14 ± 17.71	12.10 ± 11.18	17.29 ± 19.42	0.69 ± 0.19	0.42 ± 0.28
400	42.24 ± 27.25	22.65 ± 17.50	12.41 ± 10.82	16.86 ± 18.10	0.70 ± 0.19	0.45 ± 0.27
450	41.01 ± 26.82	23.98 ± 17.40	12.75 ± 10.71	16.47 ± 17.06	0.69 ± 0.18	0.46 ± 0.27
500	40.09 ± 26.22	24.99 ± 17.31	12.86 ± 10.54	16.21 ± 16.28	0.70 ± 0.18	0.47 ± 0.27

(extensive) (Table 2).

3.2. Contribution of management practices, plot characteristics and landscape metrics to CBB infestation levels

The model including only management practices as variables explained 35% of the variability of the maximum of number of infested

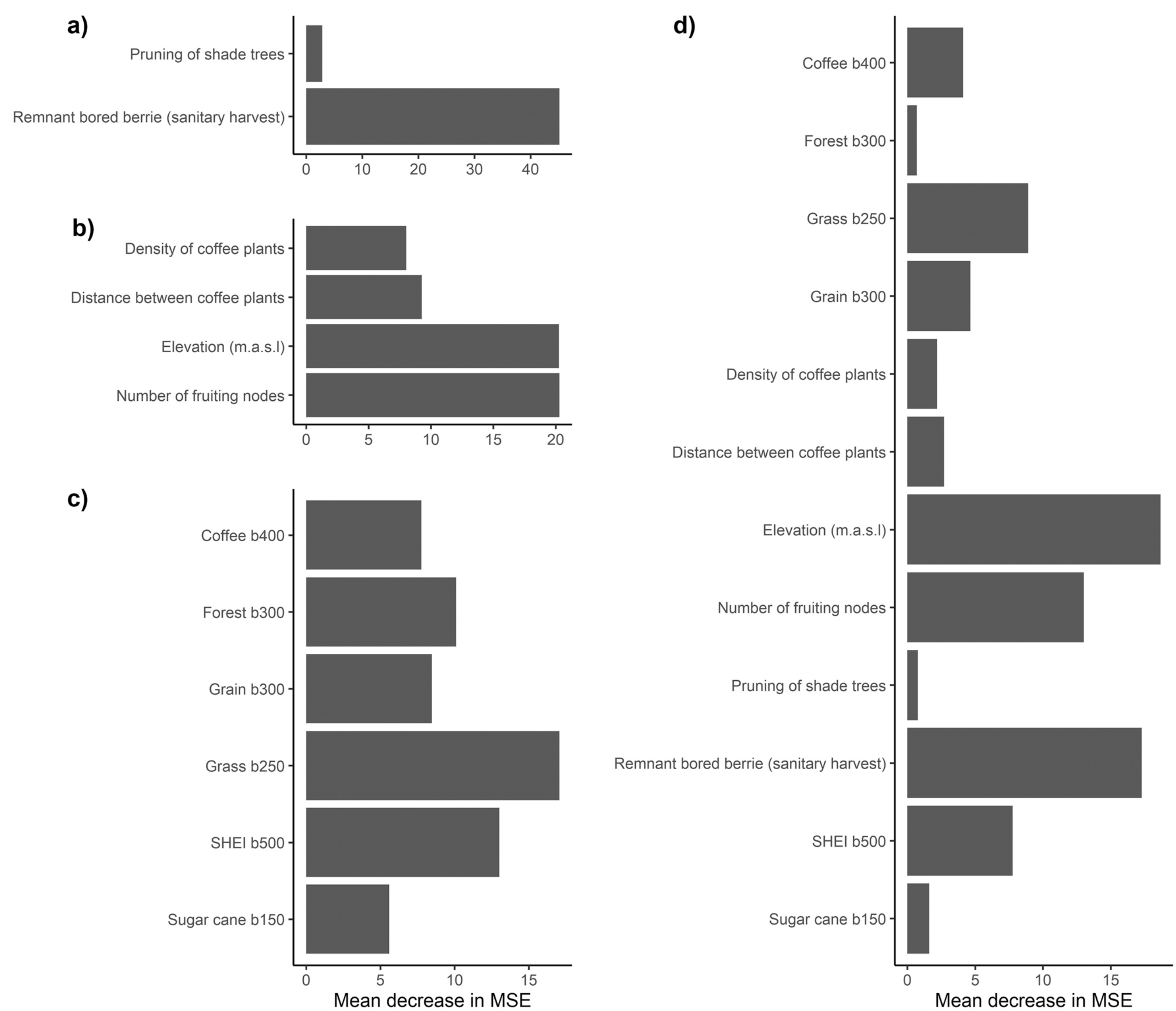

Fig. 3. Relative importance of explanatory table of variables (a) management, (b) plot characteristics, (c) landscape and (d) landscape+plot+management in explaining the variance of maximum of bored berries.

berries. The number of remnant infested berries and the frequency of shade tree pruning were the only variables contributing to the explained variance (Fig. 3a). The frequency of plot weeding, the use of *B. bassiana*, the use of coffee berry borer traps, and the application of insecticide did not show any contribution.

The model including only the plot characteristics as variables explained 42% of the variability of the maximum number of infested berries. The number of fruiting nodes and elevation were the most important variables explaining the variance, followed by the distance between plants and plant density (Fig. 3b). Shade characteristics of the plot (type and percentage) did not have any significant contribution to the explained variance and neither did the age of the plantation, the variety of coffee, the height of the plants, or the distance between rows.

The model including only the landscape metrics as variables explained 27% of the variability of the maximum number of infested berries. The best explanatory variable combination was composed of the percentage of pastures at 250 m, the Shannon evenness index at 500 m, the percentage of forest at 300 m, the grain metric at 300 m, the percentage of coffee at 400 m, and the percentage of sugar cane at 150 m (in order of importance) (Fig. 3c).

Finally, a combination of variables from the three tables (landscape + plot + management) in the most complete model explained 48% of total variability of the maximum number of infested berries. The variables with the greatest weight were plot elevation, the number of remnant berries (i.e., sanitation harvest) and number of fruiting nodes, followed by landscape metrics such as percentage of pastures at 250 m and Shanon evenness index at 500 m. Variables making smaller contributions were the variable's grain at 300 m, the percentage of coffee at 400 m, the percentage of sugar cane at 150 m, the distance between plants, and the plant density. In this model the least important variables were the frequency of shade tree pruning and the percentage of forest at 300 m. The contribution of this latest variable was more important than the contribution of the percentage of coffee at 400 m, the grain at 300 m, and the percentage of sugar cane at 150 m in the landscape metrics model (Fig. 3d).

3.3. Unique contributions of each table of explanatory variables and joined variance

Partial models indicated that the plot characteristics considered alone, i.e., when controlling for landscape and management tables, only explained 17% of the 42% of the explained variability of maximum number of infested berries obtained with the plot model. Landscape metrics alone explained only 6% of the 27% of explained variability of the landscape model (Fig. 4). Management strategies alone explained 3% of the 35% of explained variability of the management model. Indeed, 48% of the total variability is due to the joined contribution of plot, management, and landscape characteristics.

3.4. Partial relationships

The maximum number of infested berries was negatively related to elevation, to increase in the percentage of land in pastures at 250 m, to Shannon evenness index at 500 m, to distance between plants and to the percentage of forest at 300 m. In contrast, the maximum number of infested berries showed positive relationships with the number of remnant bored berries, the number of fruiting nodes, the percentage of coffee at 400 m, and the frequency of shade tree pruning. The planting density and grain index showed a quadratic relationship, while the percentage of sugar cane was highly variable with a negative trend (Fig. 5).

4. Discussion

In our study, we used a multiscale approach to assess the effect of crop management practices at plot scale, of environmental variables

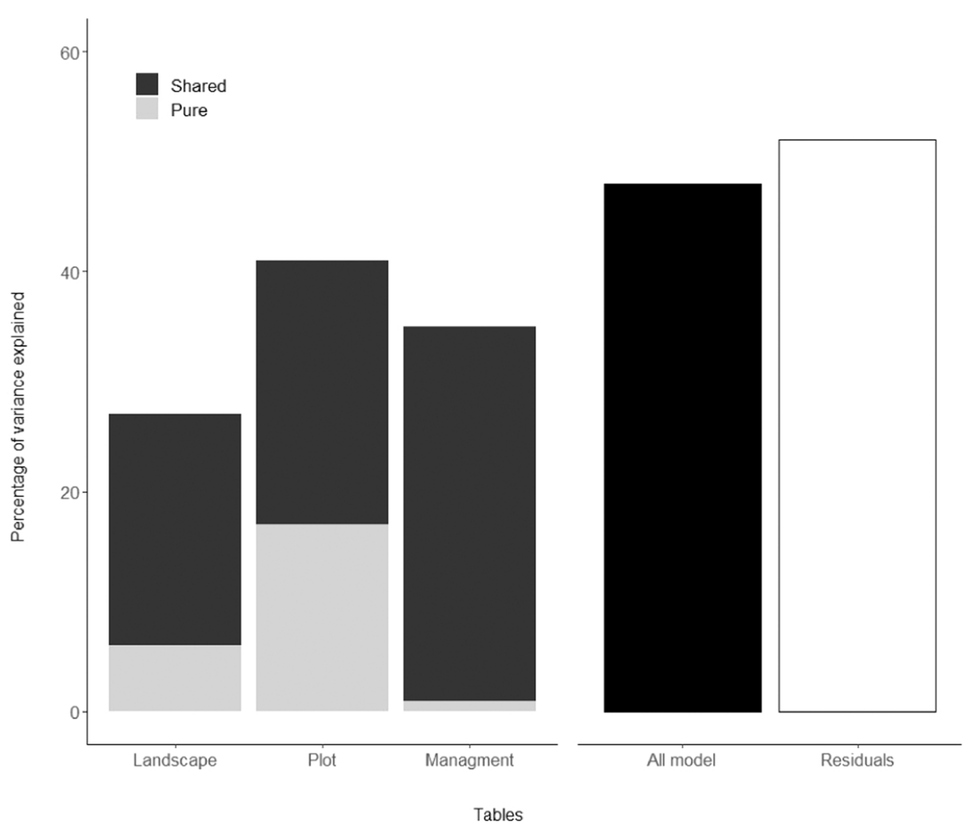

Fig. 4. Pure (light gray) and shared (dark gray) contribution of landscape, plot and management table of variables, as the total explained (black), and the unexplained (white) variation of infested berries.

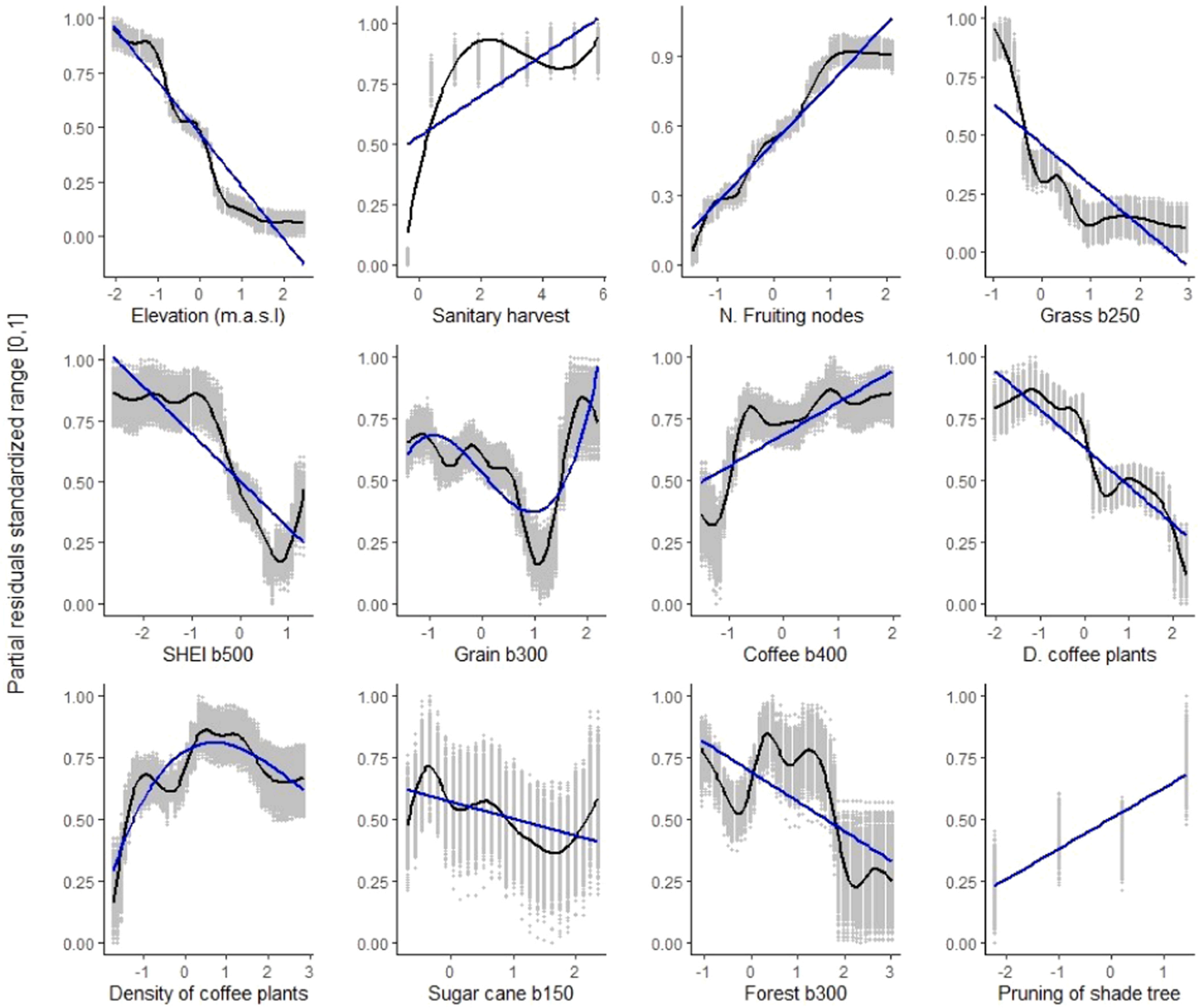

Fig. 5. Partial relationships between maximum of infested berries and each of the management, plot and landscape variables that maximize the explained variance. Black line is the average of the relationship based on the 1000 iterations of the models. Blue line indicates the trend of the relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

believed to operate at plot scale, and others operating at the landscape scale, as well as their joint contributions on the incidence of berries infested by CBB. We found consistent evidence that factors operating at the landscape level were as important as those operating at plot scale only (including crop management practices) to explain the incidence of infested berries in coffee systems. Crop management practices, plot characteristics and landscape characteristics had interactive effects that reduced the number of infested berries. We found that plot and landscape characteristics favoring coffee plant concentration (like higher number of fruiting nodes, percentage of coffee area) and CBB dispersion (landscape homogeneity based on Shannon Evenness Index and grain index) are correlated with higher maximum numbers of infested berries. We also found that plantations at higher altitudes were less affected by CBB.

We found that the portion of the variance of the maximum number of infested berries that was explained by joint effects of each group of variables (management, landscape context and plot characteristics) was more important than the part of the variance that was explained by each group's single effects. This result emphasized the importance of considering different spatial scales in order to explain the variation of the level of infested berries at the plot scale. Considering each group of variables separately, more than half of the explained variance was due to joint contribution among all the variables. This was most obvious for the group of variables related to management, which only explained 3% of the total variance. Our results confirmed that to develop a pest management strategy at the local scale, it is important to consider the effects of both local and landscape factors on pest abundance (Rusch et al., 2011).

At the plot scale, the most important variables (to explain the level of infested berries) were elevation, number of fruiting nodes, planting density, and the distance between plants. Surprisingly, there was no effect of the percentage of shade or the shade type on CBB infestation levels. More shaded systems have often been reported to increase CBB infestation levels (Bosselmann et al., 2009; Mariño et al., 2016) in comparison with full sun systems, even though some studies failed to find clear effects due to the interaction between shade and other components of the system (Soto-Pinto et al., 2002; Teodoro et al., 2008). Mariño et al. (2016) observed higher infestation rates under shade conditions, with fewer individuals inside berries. Indeed, shade tends to buffer temperatures and to maintain humidity close to the optimum for

CBB survival (Damon, 2000). In our study, the absence of an effect of shade could have been due to temperature and humidity in the study area. Turrialba temperature varies between 24 and 29 °C and its average relative humidity is 85%, both favorable for CBB with an optimal development thermal range between 15 and 27 °C (Jaramillo et al., 2010; Azrag et al., 2020) and close to 90% relative humidity (Baker et al., 1992). Moreover, the level of shade considered in the study (between 0% and 59%) might have not been sufficiently contrasting to observe significant difference.

We also showed how certain management practices, including whole-farm sanitation harvest and pruning of shade trees, explained the variability of maximum number of infested berries, while others, such as number of cycles of weeding, use of CBB trapping, applications of chemical insecticides, and the use of *B. bassiana*, did not. Timely harvest of coffee and the collection of residual fruits on the plants (i.e., whole-farm sanitation) are important practices known to reduce local CBB populations that would otherwise be available to colonize berries in the next CBB generation in a plantation (Vega et al., 2009; Johnson et al., 2020). A recent study based on a simulation model of control of CBB confirmed that intensive harvesting of coffee was the most effective control practice for reducing CBB infestations in Colombia and Brazil (Cure et al., 2020). Moreover, the use of CBB traps and of *B. bassiana* applications could also be efficient practices to control CBB population when they are adequately deployed (Vega et al., 2009; Aristizábal et al., 2016; Escobar-Ramírez et al., 2019; Johnson et al., 2020). To be efficient, traps have to be used during the flight periods of female CBB during the period when coffee bushes are in their unproductive season. In addition, these traps are more effective when used in coffee regions with a marked dry season and clustered flowering events, as CBB massive emergence occurs in short windows of time. This is not the case of our study area where rain is present across all year resulting in multiple flowering events and a longer period of fruit availability *Beauveria bassiana* is also more efficient under shade conditions, which produce higher humidity rate that favor the growth of this entomopathogen fungus. In our analysis, we could not provide detailed information on the use of CBB traps and of *B. bassiana*. This lack of information could partly explain the absence of effect of these strategies as farmers may not implement them appropriately. However, farmers follow Icafe recommendations to implement these management practices (e.g. 20 traps/ha after harvesting or even during the harvest season, http://www.icafe.cr/wp-content/uploads/revista_informativa/Revista-I-Sem-07.pdf) so we assume that those farmers who declared to follow Icafe recommendations were doing them correctly.

Our study confirmed for the first time that there was an effect of a certain configuration landscape metrics (i.e., grain index at 300 m and Shannon evenness index at 500 m) that significantly affected the maximum number of infested berries. We also found significant effects on CBB infestation levels for other landscape composition metrics (i.e., % of land in forest, coffee, pasture, or sugar cane), in line with results of Avelino et al. (2012), with the exception that they did not find any significant effect of land area in sugar cane on the incidence of infested fruits and the action scales were not the same. In fact, Avelino et al. (2012) found a significant influence of the percentage of landscape in coffee at 150–200 m of in pasture between 100 and 350 m, and of forest at 150 m, whereas in this study we found significant effects for these land use types at 400 m, 250 m and 300 m, respectively. The main differences between our works and Avelino et al. (2012) were in relation to the land area in coffee and forest. These differences with our works, may be caused by the fact that Avelino et al. (2012) explored simple linear relationships between the incidence of infested berries and landscape composition metrics, but did not consider the covariation of the other metrics, including the configuration metrics (grain index and Shannon evenness index). Among the five most important explicative variables of bored berries incidence, there are two from plots (altitude, number of fruiting nodes), one from management (remnant fruits) and two from landscape (% of pasture 250 m, SHEI). Our study confirms the finding that some landscape characteristics can override the impact of field level management practices (Kebede et al., 2019).

The relationships between variables occurring at different spatial scales and the incidence of infested berries are largely explained by CBB's biological traits. These relationships can occur at different scales, favoring the incidence of the infested berries, or not. At the plot scale, variables like the number of nodes with berries, the distance between plants, and the density of coffee plants are important variables explaining the maximum number of infested berries that can be directly related to fruit production and availability, and to the resource concentration hypothesis (Root, 1973). At the landscape scale, positive partial relationships with the percentage of the landscape in coffee and the highest grain index and negative partial relationships with the landscape percentages of forest, pasture, and sugar cane, and the Shannon evenness index, suggest that homogenous landscapes dominated by coffee favor CBB. More heterogenous landscapes can act as barriers inhibiting CBB displacement such that dispersing CBB female adults would expend more energy searching for coffee plantations, causing an increase in mortality (O'Rourke and Petersen, 2017). Pests with limited dispersal capabilities, such as CBB, may be more affected by landscape diversification than robust dispersing species when resources are limited, For CBB limited resources occur as after harvest. In contrast, plots that are adjacent with other coffee plantations (which is characterized by the grain index) would experience decreased time spent in dispersal to find new, adequate coffee habitats.

The partial relationships found between the maximum number of infested berries and landscape or plot variables are in agreement with O'Rourke and Petersen's (2017) extension of the resource concentration hypothesis of Root (1973) to a landscape scale. This extension of Root's hypothesis predicts that herbivorous insects will be more abundant in large patches of their host plants because these patches are easier to locate, and herbivores will stay longer in big patches (Root, 1973). On the one hand, the observed influences of factors such as number of berry nodes, the distance between plants, the density and percentage of land devoted to coffee all support the idea of resource concentration acting at a local scale (Root, 1973). On the other hand, landscape factors such as the Shannon Evenness Index, the grain index, the percentage of the landscape in forest, pasture, or sugar cane support importance of landscape-scale mechanisms. In addition, heterogenous landscapes can increase the abundance and diversity of generalist natural enemies (e.g., birds, ants) in surrounding areas devoted to other uses (Bianchi et al., 2006), and such diverse landscapes can favor top-down regulation of crop pests (Aristizábal et al., 2019; Escobar-Ramírez et al., 2019). The presence of forest in the landscape can favor ant and bird populations and hence their regulation of pests.

Elevation had the greatest weight towards explaining the variance of the maximum number of infested berries. Low altitude coffee areas are characterized by higher temperatures, as well as higher relative humidities, which can influence the thermal tolerance of CBB (Jaramillo et al., 2009; Hamilton et al., 2019; Giraldo-Jaramillo et al., 2018), as well as the availability of resources (Damon, 2000). Indeed, it is known that Arabica coffee, grown at low elevations, is very attractive to *H. hampei*, possibly due to a weakening of the plant, which grows best at altitudes above 1200 m. Our study was conducted at low altitudes (between 613 and 1182 m) that are close to the minimum needed to cultivate Arabica coffee.

We also found a positive partial relationship between the maximum number of infested berries and the frequency of shade tree pruning. Current IPM recommendations for CBB control in Central America include pruning to ventilate the coffee plantation and facilitate the penetration of sunlight, which would increase the speed of drying of any residual berries that have fallen to the ground, thus reducing the survival of any CBB stages present in these berries. Our results, indicate otherwise. A higher frequency of pruning of coffee shade trees can increase temperature and lower relative humidity, favoring CBB by shortening its developmental time and increasing adult female emergence (Baker et al., 1992). Shaded areas can also promote survival of *B. bassiana* and consequently increase CBB mortality. Moreover, since shade trees can enhance predation on CBB through habitat provision for natural enemies (Morris and Perfecto, 2016; Karp et al., 2013; Martínez-Salinas et al., 2016; Aristizábal and Metzger, 2019), it may be that frequent pruning may reduce favorable habitat for CBB predators. However, shade effects on CBB are still to be better clarified, for example Mariño et al. (2016) found a higher incidence of infested berries in plots under shade, but with a lower total population of CBB per berry. Finally, shade tree pruning may interact with other practices, and it is related with other pests and diseases such as coffee leaf rust, and management decisions by farmers must consider these interactions.

5. Conclusions

This study allowed us to identify factors that contribute to the reduction of the number of infested coffee berries in our study region. We showed that more heterogeneous landscapes, with more forest and less aggregated coffee plots, combined with a lower coffee plant density (i.e., plants with greater distance between them), a lower pruning frequency, and good sanitation harvest practices (that reduce the number of residual coffee berries after harvest) result in fewer infested berries. Based on our findings, we think that an integrated and area wide CBB management plan should consider influences that act at multiple spatial scales as well as the coordinated action among farmers that share the same landscape. Coordinated management decisions for pest control among neighbor farmers would result in an efficient control of pest populations, particularly for mobile pest like CBB, a reduction in production costs and a reduction of the negative impacts of crop production to the environment. Our results confirm that to develop a pest management strategy at local scale it is important to consider the effect of both local and landscape factors affecting pest abundance. The recognition of the importance of heterogenous landscapes and coordinated control and management among farmers should be accompanied by the development of incentives that encourage farmers to do so (Brévault and Clouvel, 2019).

Our approach to analysis is a good approximation to understand the response of the CBB to its environment at different spatial scales. This approach is widely used in the field of ecology and conservation biology to assess the independent or combined effects of environmental factors that contribute to the patterns of ecological communities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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