Effects of local and landscape scale factors on ant diversity and biocontrol of the coffee berry borer in Colombia

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Ph.D. Dissertation

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Summary

The coffee berry borer –CBB- (*Hypothenemus hampei*) is the economically most important pest of coffee worldwide. Within the Integrated Pest Management –IPM- strategy for this borer, the biological control component has received great attention, particularly under a classical biological control approach. However, despite the large numbers of relevant papers on this topic it is still unknown i) what are the most effective biocontrol agents and which crop management practices are most successful. Furthermore, despite the growing evidence on the importance of the landscape for natural enemies diversity and pest control services in agroecosystems, knowledge gap of CBB biocontrol is still big. We need to answer questions such as i) does spatial heterogeneity in coffee landscapes affect diversity patterns of CBB biocontrols? and ii) how do local and landscape-scale factors (and their interactions) affect fruit infestation by the CBB? This dissertation aims to fill the above-mentioned research gaps in three main chapters.

In *chapter 1* we reviewed the most relevant peer-reviewed literature on CBB biocontrol published between 1990 and 2017 in order to compare control efficacy among taxonomic groups and to identify how crop management practices at the farm level and landscape-scale factors affect biocontrol success. We found that different taxonomic groups, mainly fungi, ants, microhymenoptera and nematodes, provide successful control. Ants were the enemy group with the highest number of published papers on effective CBB control under field conditions being up to 6 times more effective to reduce pest impact than experimental treatments without ants. Over 40% of the studies showing effective CBB control do not disclose information about the use of agrochemicals or shade management, which makes evaluations of potential biocontrol difficult. Only one out of 22 the studies showing successful biocontrol explicitly included landscape-scale factors in their evaluations for CBB success.

Based on the knowledge gaps found in the literature review, we assessed in *chapter 2* the effects of local and landscape-scale management practices on the diversity of ants, which are known to be successful CBB biocontrol agents. Using tuna baits, we sampled coffee-foraging ants in three land-use types along an agricultural intensification gradient (forest, shaded coffee and unshaded coffee) in a Colombian coffee landscape. Results showed that ant species turnover among plots was reduced with management intensity (i.e. loss of

shade cover), from a mean species richness of 14.5 (± 1.32) in forest to 10.0 (± 1.23) species in unshaded coffee plantations. We also found the highest species habitat specificity in forest and the lowest habitat specificity by dominant ants in unshaded coffee when around a 40% of forest was bordering the plots. Our results suggest that preserving the forest in the coffee agroecosystem could enhance ant diversity at the landscape scale through increasing species turnover among coffee plantations, and by decreasing habitat specificity of highly dominant ants in unshaded coffee plantations.

We evaluated in *chapter 3* the importance of ant presence, together with management practices at local and landscape-scale, on CBB attack rates. Results confirmed the importance of ants to control and reduce CBB infestation rates as we found a 16.9 % relative increase in fruit infestation rates when ants were excluded from coffee branches. Additionally, this chapter showed that CBB biocontrol management should be implemented in coffee agroecosystems and landscapes at different spatial scales. Specifically, we found that local conditions such a higher number of twigs and the absence of shade, were related with lower CBB infestation rates. At the landscape-scale, larger plot perimeter sections bordering other crops, increased infestation rates in the studied region.

In conclusion, we demonstrate the importance of natural enemies to provide autonomous pest control in a Colombian coffee landscape. We showed that i) ant presence and diversity, and ii) the interaction of local (i.e., number of twigs in the ground, tree presence) and landscape factors (i.e., non-cropped area surrounding the coffee plantations) should be considered and explicitly managed in areas where coffee is the dominant crop. We propose that coffee management in this region should be oriented to i) promote coffee-foraging ants and forested habitat to maintain high ant species turnover in coffee landscapes, and additionally, ii) combine management practices at local and landscape scales to better control CBB infestation. In this dissertation we also highlight the importance of implementing a Conservation Biological Control approach in the IPM strategy for CBB control, which seeks to enhance abundance and efficacy of natural enemies at local and landscape scale.

CHAPTER 1

General Introduction

Since crops domestication, humans have been fighting associated pest and diseases that even until present days (and developing technologies), threat and put under risk plant food resources and other related products used to fulfill human needs (Barbosa, 2003).

In the last decades, academics and managers have been particularly looking for pest control strategies that provide sustainable alternatives to conventional practices. Such alternatives seek to reduce the negative impacts by chemical pesticides related with pest resistance, depletion of non-target organisms (i.e., natural enemies for pests), and threats to human health and the environment (Stenberg, 2017). An important body of research on this regard, is mainly based on biological pest control (Eilenberg et al., 2001). A relatively new, but significant approach inside the biological control discipline, is “conservation biological control” which aims to support populations of pest natural enemies present in the agroecosystem and promote their success over the pest (Begg et al., 2017; Jeanneret et al., 2016). Non-cultivated habitats in agricultural landscapes support population of natural enemies (Tscharntke et al., 2007). A proper management of non-cultivated habitats would be expected to boost natural enemy populations and thus reduce pest impacts. However, despite the abundant evidence on the importance of natural enemies conservation for biological pest control in European countries, there is a big gap of information in this regard for globally important tropical cash crops, like coffee.

Due to its ecological context (i.e. growing in tropical areas with high biodiversity, overlapping with important biological hot-spots), the international interest on the product, and to the socio-economic importance for the producer countries, coffee agroecosystems present an important and interesting model to evaluate agroecological dynamics (including pest controls) that will inform managers working in this and other similar systems. Within successful biocontrol agents, ants have shown to be particularly effective to control pests in coffee plantations mainly because of their ubiquitous presence in the coffee crops and their high predatory capacity over other invertebrates in these settings (Morris et al., 2018)

Although a rich volume of literature and research on coffee pests control is available, production of this crop still face serious biological threats that represent a constant risk over this multimillionaire industry (Infante et al., 2014; Vega et al., 2015). Among significant coffee pests, the coffee berry borer –CBB-, *Hypothenemus hampei* Ferrari 1886 (Coleoptera: Scolytinae) is responsible for the highest coffee yield losses around the world. Nevertheless, CBB infestation dynamics also presents many gaps in our understanding in spite of its tangible pervasive effects (Aristizábal et al., 2016; Avelino et al., 2012). According to our knowledge, such lack of information can be mainly summarized in three general issues:

> First, an actualized synthesis of natural enemies of the coffee berry borer is not available yet; additionally, there is a lack of a standardized methodology for the evaluation of CBB control agent success that, along with a clear evaluation mechanism (i.e., rigorous, replicable and comparable), that allows to assess CBB biocontrol agents success from available specialized literature.

> Second, even when CBB biocontrols diversity patterns in response to management factors at the farm-level (local scale) are well documented, particularly for ants (De la Mora et al., 2013; Livingston et al., 2013), information is still scarce regarding how spatial heterogeneity affects diversity patterns of these same CBB potential controllers.

> Finally, it has not been assessed *in situ* how local factors (including the presence/absence of ants), landscape factors and, mainly its interactions, affects CBB infestation rates.

The present dissertation, performed in Caldono-Cajibío, one of the most important coffee regions in southwestern Colombia, looks forward to fill the above-mentioned research gaps by presenting in *chapter 1* of this investigation, a review of the most relevant peer-reviewed literature on CBB biocontrol agents published between 1990 and 2017. Specifically, this first section uses up to date publications and provides an assessment on the success of biocontrol agents by comparing the effects of CBB in presence (and absence) of natural enemies. For this evaluation, we provide rigorous criteria to better define success of the different biocontrols tested in the literature. Additionally, and for a first time in a review, we systematize and evaluate the number of publications testing the effects of crop management practices at the farm level and how landscape-scale factors are affecting biocontrols success. Among others, results of this introductory section highlights the lack of studies analyzing the relative importance of local and landscape management (i.e. agricultural practices) for entomopathogens, invertebrate and vertebrate predators, that may help to reduce CBB pest pressure under more sustainable approaches. Also, this section allows concluding that from all the biocontrols assessed in the specialized literature, ants are one of the most effective invertebrates group controlling CBB specifically.

Using conclusions from chapter 1 regarding ants importance and the lack of studies incorporating landscape scale variables to better control CBB, *chapter 2* evaluates the effects of local and landscape management practices over ants diversity. Here, a field design using ants attractants was implemented to understand how i) α (at the bait and coffee plantation-level); β diversity (between-baits and between-coffee plantations level) components of ant richness; and, ii) ants species habitat specificity, change between land-use types and the percentage of forest surrounding the evaluated coffee plots. Additionally, the abundance of ants with potential as biocontrols is compared between land-uses (forest, shaded and unshaded coffee). Results of this chapter allow concluding that keeping forest in Colombian coffee-producing sites could enhance ant diversity at the landscape scale through increasing β diversity –or ant's species turnover– among coffee plantations. Particularly, unshaded-plots specialists and dominant ant species (adapted to "hot-climate" conditions) decreased in relation to an increase in the proportion of forest surrounding studied coffee plots.

To incorporate the main findings from previous chapters and to specifically test which factors are influencing CBB prevalence in a Colombian coffee plantation, *chapter 3* of this dissertation uses extensive field work data and mathematical modeling to explore how the exclusion of ants, the variation of local factors, landscape characteristics and their relevant interactions, affect CBB infestation rates. Results of this final chapter allow confirming ant's importance to control and reduce CBB effects in coffee bushes. Additionally, this chapter shows that in order to reduce CBB negative effects, management actions at different scales (such as the number of twigs in the ground, tree cover presence and the amount of coffee plot perimeter bordering non-cropped areas) should be implemented (in an interactive fashion) in coffee agroecosystems.

Finally, and as a parallel/transversal objective of the present dissertation, each chapter provides general managerial recommendations based on main findings. We speculate such guidelines will help to better inform different players in the coffee industry and thus, reduce pest threats and increase more ecologically friendly and sustainable solutions for this significant crop.

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CHAPTER 2

Biological control and natural enemies of the coffee berry borer – a review

Abstract

Coffee is one of the most important commodities globally and the coffee berry borer (CBB) is its main pest, causing losses of more than half a billion dollars annually. In this systematic review, we quantify the available evidence of successful biological control in coffee agroforestry. There is a recent research trend of switching from the traditional focus on classical biological control (i.e. introducing parasitic wasps), to conservation biological control, considering a broad range of enemy groups inhabiting the cropping system. We found 22 papers proving CBB biocontrol success in the field and 22 studies suggesting potential biocontrol. Most papers showed effects of fungal infections, followed by papers on ant communities, parasitic Hymenoptera, birds, and nematodes. With respect to local coffee management, arboreal canopy cover providing shade as well as organic practices enhances biocontrol success. Landscape-scale studies are almost missing, although CBB predation by birds can be significant and may provide benefits from the presence of forest patches in the surrounding. Insectivorous birds effectively reduce yield losses by CBB, whereas in many other taxa there is a need for identifying economic threshold levels. In conclusion, understanding and implementing prophylactic coffee management to reduce CBB pest pressure require of more studies focusing on conservation biocontrol, by modeling and analyzing the relative importance of local and landscape management for fungal infections, invertebrate, and vertebrate predators.

Keywords: biological control, *Hypothenemus hampei,* coffee pest, literature search.

Introduction

Coffee is one of the main commodities worldwide with revenues of ~$173 US billion dollars (2012 data, FAO 2015; Aristizábal et al. 2016). About 80 countries produce coffee and almost a half of the coffee yield (~8.5 million tons/year) comes from just three nations: Brazil (28%), Vietnam (10%) and Colombia (8.3%) (ICO 2017). Coffee represents the main income source for about 20 million families, most of them smallholders in rural areas of tropical developing countries, where they are most vulnerable to pests and diseases that reduce yield quantity and quality (UNDP, 2011).

Coffee crop faces serious diseases and pest problems. The coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae), is considered the main economic pest, negatively impacting crop yields all over the world with losses surpassing more than $500 million annually (Vega et al., 2015). The CBB adult female drills the fruit into the calyx and causes seed damage by forming galleries in the coffee seed to lay her eggs. Upon hatching from the eggs, the larvae continue the damage by consuming the seed, negatively affecting production (seed weight), coffee quality and yield price (Aristizábal et al., 2016; Duque and Baker, 2003; Wegbe et al., 2003). Losses due to CBB in Brazil, the first producer worldwide, have been estimated around US$215–358 million annually (Oliveira et al. 2013, FAO 2015).

CBB control practices have been combined in Integrated Pest Management (IPM) programs and include cultural, biological and chemical control, as well as post-harvest sanitation practices (Aristizábal et al., 2016). IPMs need periodical reviews in order to evaluate the effectiveness of its biological components, kind of environments, social contexts for coffee production and changing markets. For instance, biological control of the CBB (i.e. the use of natural enemies-based techniques to control the borer) is a component of the coffee IPM programs, which gained an important role after strong restrictions in the use of synthetic pesticides, to reduce risks on human and environmental health as well as pest resistance (Monzón et al., 2008).

Biological control practices are centered on three main approaches: classical biological control (i.e. introduction of alien natural enemies to attack alien, invasive pests), biological control by conservation (i.e. protection and enhancement of biological control agents in the agroecosystem) and augmentation of enemies for mass release in the crop (Aristizábal et al., 2016; Begg et al., 2017; Eilenberg et al., 2001). The most widely investigated CBB enemies are 1) entomopathogenic fungi like *Beauveria bassiana* and *Metarhyzium anisopliae*, 2) nematodes in the genus *Heterorhabditis* and *Steinernema*, 3) parasitic wasps like *Cephalonomia stephanoderis, Prorops nasuta* and *Phymastichus coffea*, and 4) generalist predators (i.e. ants, birds, trips, anoles and coleopteran) (Aristizábal et al., 2016; Bustillo et al., 2002; Damon, 2000; Jaramillo et al., 2005; Vega et al., 2009a).

Among the biological control practices, classical biological control techniques have been widely explored for the CBB by introducing and augmenting the parasitic wasps *C. stephanoderis, P. nasuta* and *P. coffea* (Vega et al., 2015). Also, the application of *B. bassiana, M. anisopliae* and *Steinernema carpocapsae* as biopesticides has been successfully translated into commercial products sold in the market (Aristizábal et al., 2016; Pava-Ripoll et al., 2008). However, biological control by conservation strategies has not yet been implemented in the IPM for coffee, while there are examples from other crops (Barbosa, 2003; Begg et al., 2017; Gurr et al., 2000; Landis et al., 2000)

Although biological control is a safe and wildlife-friendly alternative option, success is variable and context-dependent (Cowan and Gunby, 1996; Wilson and Tisdell, 2000). The mixed outcomes and uncertainty make farmers reluctant to implement biological control and conservation biological control as well, as a regular practice of CBB control (Jeanneret et al., 2016). Therefore, it is an important issue to identify and analyze the conditions under which CBB biocontrol agents are effective, as well as trying to uncover patterns and alternative models.

Biocontrol success has been studied with two complementary approaches based on either field experiments or economic criteria. Comparing results of the natural enemy-treatment with the results in the control without natural enemies helps to understand the contribution of natural enemies to control CBB. The economic criterion with an economic damage threshold focuses on a pest population density that causes a damage level (Wegbe et al., 2003).

CBB biocontrols are affected by the crop management at the farm level and by landscape factors in the coffee agroecosystem (Karp et al., 2013; Vega et al., 2009b). Shaded crops have been related to higher CBB abundances, however, this is not always supported and contrary outcomes have been reported (Baker et al., 1989; Jaramillo et al., 2013). Moreover, the presence of tree shade has been also related to a higher success by *B. bassiana* (Aristizábal et al., 2016), higher rates of predation by ants (Armbrecht and Gallego, 2007) and a higher richness and abundance of natural enemies of CBB such as ants and birds (Philpott et al., 2008). Landscape factors (i.e. landscape composition, configuration, and connectivity) may also influence the effectiveness of local habitat management measures designed to improve biological control (Gámez-Virués et al., 2012; Tscharntke et al., 2007). Although these interactions are also expected to occur in coffee landscapes, few empirical studies have explored this topic (Avelino et al., 2012).

Here we provide a systematic review of the available peer-reviewed literature between 1990 and 2017, for the first time, the success of the native and introduced biocontrol agents is weighed, by comparing the effects of the CBB in presence and absence of the natural enemies. This review also evaluates for the first time the success of natural enemies and its relation to crop management factors at local and landscape scale for coffee. Specifically, this review aims to assess: 1) how many studies have tested CBB biocontrol under both, laboratory and field settings in a statistically sound ways with adequate controls in their designs; 2) how CBB biocontrol occurs by different taxa, and their particular ecological strategies; 3) whether biocontrol success occurs using the results mentioned in objectives 1 and 2; and 4) which studies showed success CBB biocontrol according to local management practices, and which of them included a landscape scale approach. Finally, future research priorities and approaches to identify measures enhancing biological control in coffee agroecosystems are discussed.

Methods

Search protocol

In June 2017, we conducted a systematic review of the literature to assess the success of natural enemies of the coffee berry borer. Based on the peer-reviewed literature from Web of Knowledge (WoK), Scopus and SciELO, we checked for studies since 1990 (for the first papers on CBB biocontrol found in WoK) until 2017. We focused the search strings on all natural enemies of CBB, their efficiency, and the influence of management of coffee agriculture at local and landscape scales to promote biocontrol of the CBB. For instance, the search string used to find papers on CBB by natural enemies was: ("*Hypothenemus hampei*" OR "coffee berry borer" OR "coffee bean beetle") AND ("natural enem*" OR "parasit*" OR "predat*" OR "prey*" OR "pathogen*" OR "entomopathogen*" OR "competit*") AND ("population size" OR "abundance" OR "crop damage" OR "survival" OR attack* OR "fruit damage" OR "mortality"). For all the different search string combinations used, see Table A.1 (Annex).

For this review, we consider only the investigations where the direct effect of the biocontrol agents on CBB was assessed (i.e. direct evidence on CBB predation, removal, parasitism, infection and/or pest displacement by biocontrol agents). We checked how many studies tested CBB biocontrol in both, laboratory and field settings. The above-mentioned studies were classified according to the taxonomic group of the biocontrol agents.

We defined three criteria for "effective" CBB control as follows. A study was considered to show "effective" control if it meets three conditions: 1) evaluations under field conditions; 2) inclusion in the design of both, an experimental treatment (i.e. exclusion of the natural enemies) and an experimental control (i.e. presence of the natural enemies), and 3) significant differences between the treatment and the control. A study was classified as evidence of "potential" control when: a) significant results were reported but there was no comparison with an experimental treatment and b) when the study does not include any evaluation under field conditions. After this re-categorization, we compared the number of published papers showing "effective" and "potential" control, considering the taxonomic group.

The different response variables in the selected papers were classified into the next five general categories, according to the trait of the pest they intended to assess: I) CBB mortality, II) CBB abundance, III) seed attack rates by the CBB, IV) penetration length into the seed by the CBB, and V) the final dry weight of the seed.

The management practices were grouped in two broad categories: the presence/absence of tree shade (i.e. shaded vs. unshaded coffee) and the regular use of agrochemicals (i.e.

conventional vs. organic -or very rare use of agrochemicals-). In addition, we considered the effect of landscape-scale parameters on the success of CBB biocontrol agents.

Finally, we classified the studies showing effective control, according to the countries where the investigations were performed and identified for each country the taxonomic groups where effective biocontrol of the CBB was reported. In this literature review, we could not perform statistical analyses due to the low number of publications for each of the analyzed variables and categories.

Results

A total of 187 papers were obtained as a result of the screening using searching engines, from which we recorded four literature reviews on CBB control (Aristizábal et al., 2016; Damon, 2000; Jaramillo et al., 2006; Vega et al., 2009b) and 44 studies assessing the effects of biological control agents on the CBB performance (Annex A.2). From these 44 resulting studies, 88% (39 papers) included an experimental treatment (Figure 1). The five remaining papers without experimental control consisted of laboratory experiments.

Fungi resulted to be the group with the highest percentage (34%; 15 out of 44) of peer-reviewed publications. The explicit inclusion of a treatment without natural enemies in the experimental design was recorded in all well-known biocontrol agents, i.e. fungi, ants, microhymenoptera and nematodes (Figure 1). The 88% of the 39 studies focused on the use of invertebrates as biocontrol agents, while studies on birds and reptiles represented only 12% (five studies). The entomopathogenic organisms represented 43% (19 out of 44) of the studies (nematodes and fungi), followed by 41% (18 out of 44) predators and 16% (seven studies) parasitoids.

Ants were the taxonomic group with the highest number of published papers providing evidence on the effective CBB control in field settings (Figures 2, 3). In general, the 23% of CBB disappeared from coffee in the treatments with ants, was about four times higher than the experimental treatment without ants. Predation by ants not only did result in a removal of CBB adults from fruits, but also of immature life stages, as well as a reduction in the percentages of seed infestation and a lower depth of CBB penetration in the fruit.

For more details about the studies supporting these findings, see Table 2. CBB seed infestation was about three times lower than the experimental treatment without birds (see Table 2), which means that birds showed to be important predators of the borer, as their presence significantly reduce seed attacks by this pest.

The fungi *B. bassiana* (Table 3) and *M. anissopliae* (Table 4), separately and combined in mixtures, were shown to exert significant control over the borer. Specifically, strains of *B. bassiana* presented the highest percentages of mycoses on CBB (61.2-80.5%, Table 5). The experimental application of *M. anissopliae* and of mixtures of *B. bassiana* with *M. anissopliae* exhibited higher CBB mortality, but it was smaller than the effect of *B. bassiana* alone. Likewise, the nematodes showed to be effective controllers of the CBB, registering mortalities above 80% by *Steinernema* sp. (88.2%) and *Heterorhabditis* sp. (82.0%). *S. carpocapsae* led to lower but significant percentages of CBB control, between 7.4 and 17.1%, for different CBB life stages (Table 6).

Two species of parasitic wasps were shown to be effective in the control of CBB. The species *P. coffea* caused 68 and 86.7% CBB mortality in the field, while *C. stephanoderis* caused 34 and 56% CBB adult mortality per fruit. The dry seed weight was positively affected by the presence of *P. coffea* and was approximately twice as heavy as those of the experimental treatment (for abundance ratios parasitoid:CBB between 1:20 and 1:10, respectively). Other benefits derived from the parasitic wasp, such as a reduction in the number of CBB eggs and immature stages per fruit, can be seen in Table 7.

About half of the studies (22 papers out of 44) provided significant evidence of effective control of CBB by natural enemies (Table 1). So far, taxa such as Coleoptera, reptiles, and thrips, have either not been tested under field conditions nor an experimental treatment has been included in the design. Hence, these taxonomic groups were reported here only as "potential" but not necessarily effective control agents of CBB (Figure 2.2). More details on these studies are further presented in Table 1.

Surprisingly, a high percentage of investigations (9 out of 22) did not disclose the management practices of the site used for the studies. The studies specifying the management practices, 46% (six out of 13) showed effective control of the CBB in organic-shaded coffee plantations. The management practices and the taxon recorded as effective CBB biocontrol agents compiled by this study for all the analyzed publications are detailed in Figure A.1 (Annex).

In spite of the importance of the spatial scale to understand the success of the CBB natural enemies, only one of the 22 studies directly showed effective control of CBB in response to landscape management (Karp et al., 2013) (Figure A.2). The remaining effective studies did not register the spatial scale, failed to included experimental treatments, or were not intended to evaluate the effect of landscape over the richness or abundance of CBB biocontrol agents. Finally, studies proving biocontrol success are concentrated in only two coffee producing countries: México and Colombia (Figure 4).

Discussion

In our systematic review, we found that the 52% of the studies showed evidence of successful control of CBB by natural enemies. Out of these 22 studies, i) a single investigation evaluated the importance of the landscape scale, ii) 41% of the investigations did not disclose the management practices of the study site, while 45% of them showed effective control of the CBB in organic-shaded coffee plantations, and iii) studies proving biocontrol success were detected in only two countries: México and Colombia.

We had expected a larger number of studies assessing the effects of biological control agents on the CBB, since recently published bibliographies on this pest list more than 1800 references (Pérez et al., 2015). However, most of the references listed in the before mentioned study are technical reports, unpublished theses or other gray literature, which is often not peer-reviewed and not available in electronic databases. Many studies found via search engines were not included in this review, as they were reviews and model simulations, or dealt with aspects of natural enemies such as biological cycle, host-specificity, release methods, the establishment in the field, virulence, interactions between control agents, etc. Previous reviews on CBB biocontrol mainly describe pest control performance from classic biocontrol and from the use of entomopathogens organisms, both of them implemented at the farm level. In comparison to the last review on IPM management of the CBB by Aristizábal et al. 2016, the present review added 30 new studies, some of them including a conservation biological control approach and assessment of the role of the landscape on biocontrol success.

Biocontrol success

We found that biocontrol agents effectively reduce the negative impacts of the CBB through four mechanisms: i) increasing the mortality of CBB adults and ii) immature life stages, iii) reducing seed attacks by the borer, and iv) reducing the weight loss of the seeds which is the marketable product of the crop. Although not tested yet, mechanisms i) and ii) together would prevent CBB outbreaks. Not all studies on natural enemies that claimed to show effective biocontrol agents of the CBB provide strong evidence. This is, for example, the case of the widely investigated parasitic wasp *P. nasuta,* for which the studies analyzed here lack field surveys and experimental treatments in the laboratory. In contrast, the relatively few and more recent studies on birds showed effective CBB biocontrol in 100% of the studies.

Therefore, there is a need of inclusion of experimental treatments in designs and validation under field conditions (i.e. in studies on *Leptophloeus* sp., *Cathartus quadricollis, Karnyothrips flavipes* and lizards), so that the derived results can better inform the farmers on the relative contribution of biocontrol agents.

Biocontrols agents such as ants, birds, and *B. bassiana* were found to successfully control the CBB and significantly reducing CBB density below the "economic damage threshold", established in Colombia and Togo. For Colombia, the threshold level has been set to 5% fruit damage (Montes et al., 2012) and 2.34% for Togolese coffee plots, based on an average yield of 800 kg of green coffee per hectare. The economic damage threshold varies with countries and international coffee prices. The ecosystem service of CBB control, provided by birds only, has been estimated as market values (i.e. US$44–$105/ha in 2005/2006; Kellermann et al., 2008) and/or as prevented damages (i.e. calculated in US$75–US$310 ha/year by Karp et al., 2013).

Crop management practices and spatial scale: When crop management practices were specified, almost a half of the studies showed effective control of the CBB in organic-shaded coffee. This could be related to a higher abundance and diversity of natural enemies, or with a lower incidence of CBB in shaded coffee. However, these hypotheses have not been tested yet. For instance, Jaramillo et al. (2013) reported ~12 times lower CBB infestation rates in shaded than in unshaded coffee in East Africa, while Baker *et al.* (1989) did not find any effect of the tree shade on coffee infestation rates in southern Mexico.

Another farm management factor that can be affecting the pest-biocontrols interaction is the use of agrochemicals. High inputs of pesticides may deploy the establishment of introduced natural enemies (i.e. parasitic wasps) and reduce the abundance and diversity of native natural enemies (i.e. ants and spiders) (Vega et al., 2015). At least for ants, De La Mora and colleagues (2015) did not find a relationship between CBB removal by ants and agrochemical use in Mexico.

In general, complex landscapes often have higher abundance and diversity of natural enemies and more effective biological control than landscapes simplified by intensive agriculture (Chaplin-Kramer et al., 2011; Rusch et al., 2016; Tscharntke et al., 2007). But few studies analyzed the effects of local management practices and landscape-level factors on CBB natural enemy richness and/or abundances. For instance, De la Mora et. al. (2013) reported two landscape factors (forest within 200 m, and distance from the forest) predicting richness and abundance of twig-nesting and leaf litter ants in a coffee landscape in Sonocusco (Mexico). Migrant bird predators, overall, did not respond to vegetation complexity in the study of Kellerman et al. (2008), but they found that the three main migrant species controlling the CBB increased with proximity to non-coffee natural habitat patches.

Regarding the effect of landscape factors on the success of biocontrols, Johnson et al. (2010) proposed that differences in the magnitude of CBB reduction by birds within the farm may have resulted from variation in shade management and surrounding habitats, but they did not test it. De la Mora et al. (2015) found that CBB removal rates by ants on coffee plants increased with both, coffee density (a local factor) and the amount of rustic coffee within a radius of 200 m, i.e. a landscape factor. However, this study did not include proper experimental treatment (without ants) and was not included in Figure A.1.

Karp and colleagues (2013) found that the presence of forest patches in the surrounding landscape doubled CBB biocontrol, and the abundance of resident bird predators increased with tree cover. This last mentioned study also demonstrated that there is a contribution of the farmland forest cover to pest removal by birds in a simplified matrix dominated by unshaded coffee under conventional use of agrochemicals. Karp and colleagues (2013) study seems to support the prediction by Tscharntke et al. (2005) that local management measures should have a greater effect in simple landscapes compared to complex landscapes.

The CBB abundance seems to respond to landscape composition. A single published study by Avelino et al. (2012) revealed that higher CBB abundances at a local scale (217m^2 approx.) were positively correlated with the proportion of coffee in the landscape (correlation coefficients peaking at 150m radius), but negatively correlated with the proportion of pasture (peaking at 400m) and forest (peaking at 150m) in the surrounding landscape

Finally, crop management strategies to enhance natural pest control might differ depending on the specialization level of the natural enemies. For instance, Chaplin-Kramer et al. (2011) found that generalist enemies showed a consistently positive response to landscape complexity across multiple spatial scales, while specialist enemies responded more strongly to landscape complexity at smaller scales. Although not available yet, information on the particular response of generalist and specialist enemies of the CBB needs to be addressed in order to better plan an integrated control strategy for the CBB.

Biocontrol success by taxonomic group

All the taxonomic groups were represented by at least one study supporting “effective” control over the CBB, except for Coleoptera, reptiles, and thrips. The eighty eight percent of the studies focused on the use of invertebrates as biocontrol agents, while studies on birds and reptiles represented the 12% remaining. Fungi were the focus for the highest number of peer-reviewed publications, followed by ants and parasitic wasps. Therefore, the predominant CBB control mechanisms were entomopathogenicity and predation by invertebrates, followed by parasitism.

Until 2006, most of the research focused on parasitoids, fungi, and nematodes. Afterward, focus switched to the role of non-introduced organisms such as native ants, birds, coleopterans, trips, and lizards. This demonstrates a change in the approach for the CBB biocontrol, switching from classical biological control to the contribution of the natural enemies already present in the coffee habitats (i.e. conservation biological control). Benefits for coffee farmers derived from this approach include lower costs, lower logistics, fewer problems with the establishment of the biocontrol agents, and less environmental risks associated with the introduction of exotic species. The decline on research about parasitic wasps is attributed to some of the above-mentioned factors, but also to the fact that they were effective only at high parasitoid: borer ratios (1:10 and 1:5), a number difficult to afford and to keep in the field.

This review provides evidence that a "silver-bullet" approach (i.e. the use of one single biocontrol under a general setting) would not be appropriate for CBB biological control in coffee. For example, ant assemblages in the coffee agroecosystem, as well as particular native species (i.e. *A. instabilis, A. sericoseaur, P. synanthropica, Solenopsis picea* and *Gnamptogenys sulcata* in Central and South America) were highly effective controlling different damage stages and aspects by CBB and the complexity of the agroforestry systems prevents a unidimensional approach. Also, assemblages of generalist resident birds and migratory birds reduced CBB infestation effectively, being up to three times more effective than without birds. This is consistent with a review of manipulative field studies by Symondson et al. (2002) showing that, in 75% of cases, generalist, not specialist predators (whether single species or species assemblages) significantly reduced pest numbers.

Conclusions

Effective biological control of the CBB originated from different taxonomic groups in the coffee agroecosystem, in many cases native species that have found coffee habitat a suitable refuge. Hence, a successful strategy for pest control will not come from enhancing a single biological controlling species, but from understanding the benefits of the complex interactions in the system, and how they are translated into benefits for the coffee farmers (specially using a conceptual approach towards conservation biological control). Therefore, the biological control of pests in coffee farms must be developed under an IPM framework that takes into account the contribution, not only of factors such as providing habitat to enhance natural enemies, but also all the different sources of biocontrol (i.e. predators, parasitoids and entomopathogens) and the potential interactions among the natural enemies and interactions with other pest control practices, such as cultural control and chemical insecticide. Unfortunately, the effect of the combined effects of local and landscape management practices for CBB biocontrol is still little known and limited to few coffee regions in the world. In order to improve our understanding of local and landscape effects on biological control of the CBB, future studies will need to be designed under contrasting scenarios combining local and landscape factors to identify the management conditions that enhance pest regulation services by the main natural enemies in coffee agroecosystems. Additionally, economic benefits of natural control should be compared with other practices such as chemical and cultural control, in order to provide farmers with practical evidence about the real benefits of biological controls. So far, the economic benefits derived from pest control services have been quantified only for birds but is needed to evaluate the success of other native natural enemies of the CBB.

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Figures

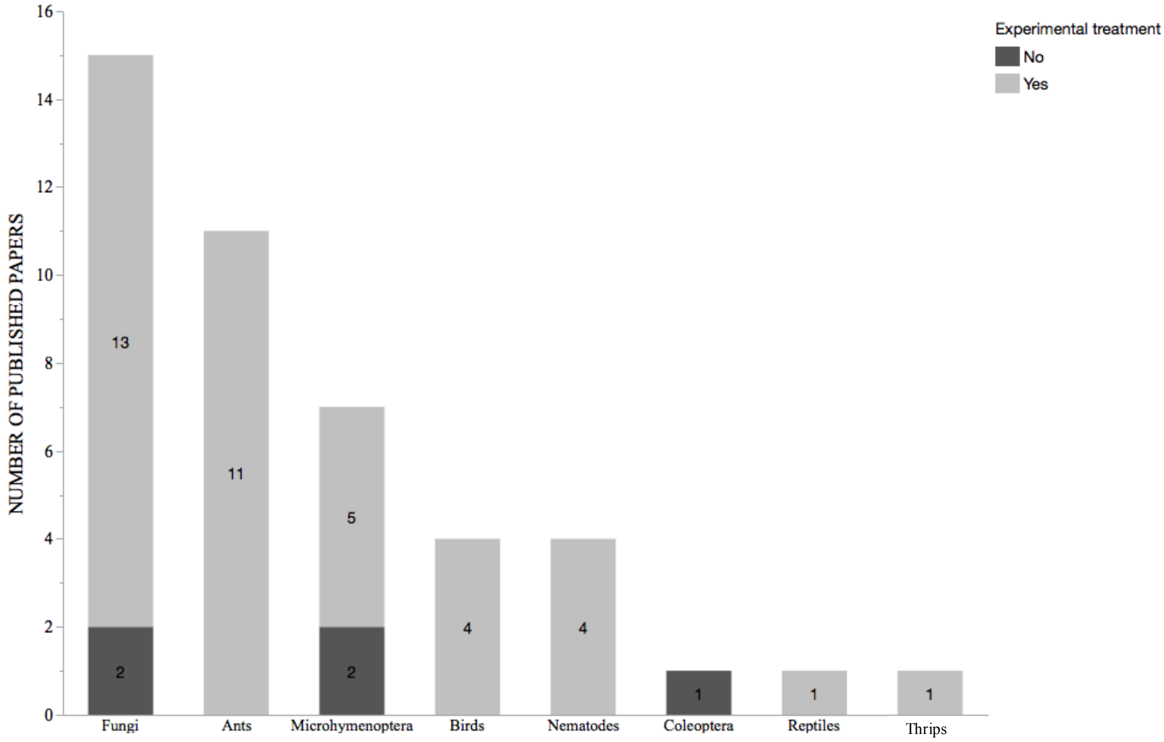

Figure 1. The number of published papers per taxonomic group, indicating how many of them have proper experimental treatments (exclusion of the natural enemies) in their experimental design (N= 44 papers, Tables S2). Note that studies without an experimental control are presented for comparative purposes, as this investigation defines studies with a control included to be effective for testing CBB biocontrols.

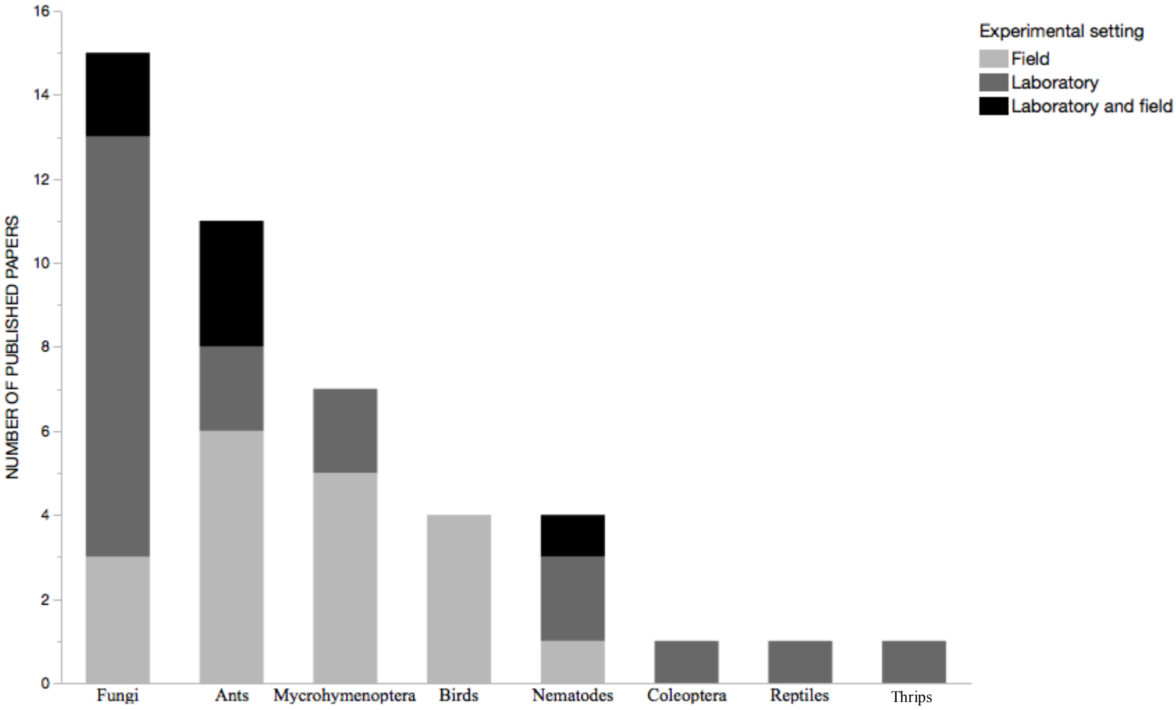

Figure 2. Numbers of published papers per taxonomic group, indicating how many studies were performed in the field, laboratory or both conditions (N= 44 papers, Tables S2).

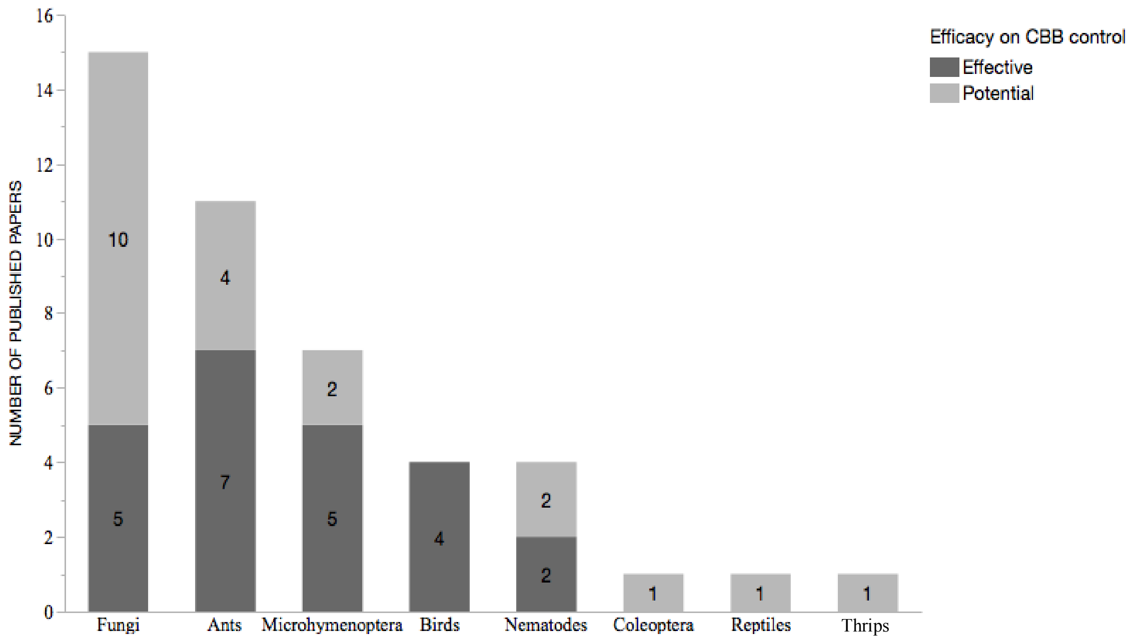

Figure 3. Classification of the 44 papers (evaluating directly the effect of a biocontrol over CBB) according to the "minimum efficacy criteria" reporting significant results on CBB control efficacy, into effective and potentially effective biocontrol agents.

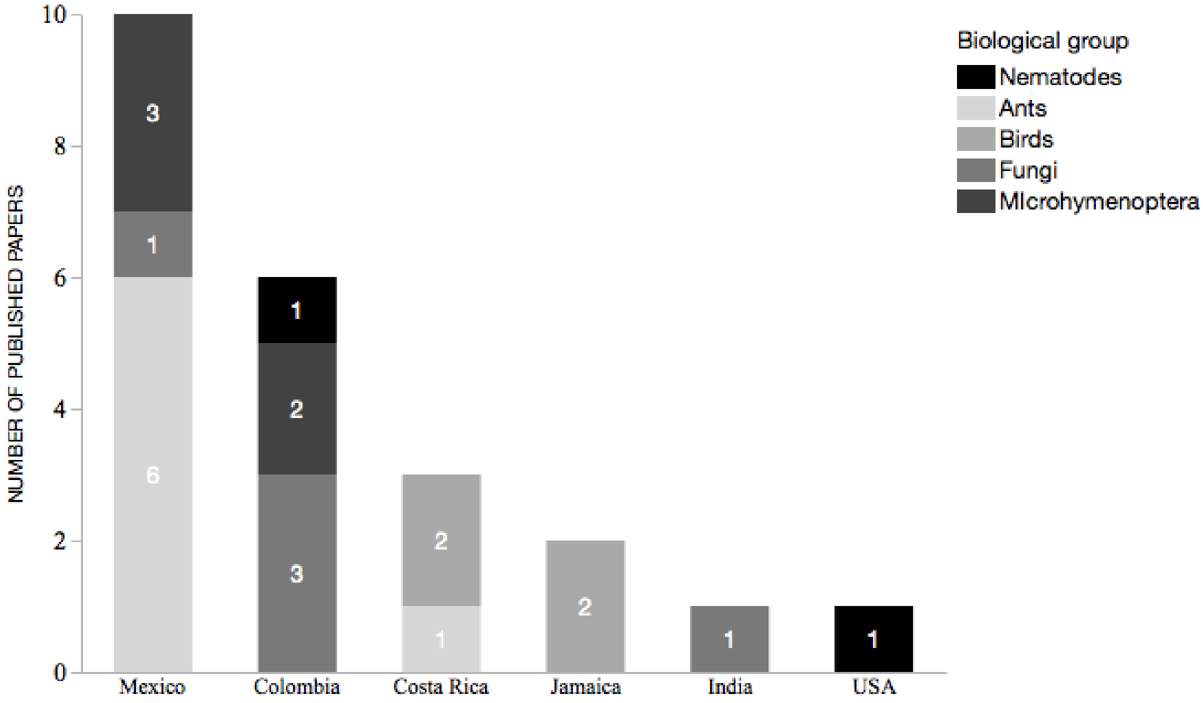

Figure 4. The number of studies (N= 22, Table S3) per coffee producer country, which has demonstrated effective control on CBB. The taxonomic groups involved are indicated.

Tables

Table 1. List of the 22 papers showing successful control of biocontrols over the CBB. These studies meet with the three criteria for a study to be considered a successful: 1) evaluations under field conditions; 2) experimental treatment (i.e. exclusion of the biocontrol agent) in the design, and 3) significant differences between the experimental treatment and the control including the biocontrol agent.

No	Year	Authors	Tittle	Controller species	Journal
1	1998	Aristizábal, Bustillo, Baker, Orozco & Chaves	Depredatory effects of the parasitoid *Cephalonomia stephanoderis* on the immature stages of *Hypothenemus hampei* in field conditions	*Cephalonomia stephanoderis*	Revista Colombiana de Entomología
2	1999	Bustillo, A.E., Bernal, M.G, Benavides, P. & B. Chaves	Dynamics of *Beauveria bassiana* and *Metarhizium anisopliae* infecting *Hypothenemus hampei* Coleoptera: Scolytidae abundances emerging from fallen coffee berries	*Beauveria bassiana*	Florida Entomologist
3	2000	De la Rosa, Alatorre, Barrera, & Toreillo	Effect of *Beauveria bassiana* and *Metarhizium anisopliae* (Deuteromycetes) upon the coffee berry borer (Coleoptera: Scolytidae) under field conditions	*Beauveria bassiana*	Journal of Economic Entomology
4	2001	Haraprasad, Niranjana, Prakash, Shetty, & Wahab	*Beauveria bassiana* - A potential mycopesticide for the efficient control of coffee berry corer, *Hypothenemus hampei* (Ferrari) in India	*Beauveria bassiana*	Biocontrol Science and Technology
5	2002	Damon & Valle	Comparison of two release techniques for the use of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae), to control the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) in Soconusco, southeastern Mexico	*Cephalonomia stephanoderis*	Biological Control
6	2004	Lara, López, & Bustillo	Effect of entomopathogenic nematodes on populations of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae), in berries on the soil	*Heterorhabditis* sp.	Revista Colombiana de Entomología
7	2005	Jaramillo, Bustillo, Montoya, & Borgemeister	Biological control of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae) by *Phymastichus coffea* (Hymenoptera: Eulophidae) in Colombia	*Phymastichus coffea*	Bulletin of Entomological Research
8	2006	Perfecto & Vandermeer	The effect of an ant-hemipteran mutualism on the coffee berry borer *Hypothenemus hampei* in southern Mexico	*Azteca instabilis* (+*Coccus viridis*)	Agriculture Ecosystems & Environment

No.	Year	Authors	Tittle	Controller species	Journal
9	2008	Kellermann, Johnson, Stercho, & Hackett	Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms	Birds (migratory warblers and resident)	Conservation Biology
10	2009	Espinoza *et al.*	The biology of *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae) under field conditions	*Phymastichus coffea*	Biological Control
11	2010	Johnson, Kellermann, & Stercho	Pest reduction services by birds in shade and sun coffee in Jamaica	Birds	Animal Conservation
12	2010	Larsen & Philpott	Twig-nesting ants: the hidden predators of the coffee berry borer in Chiapas, Mexico	Twig-nesting ants	Biotropica
13	2011	Vera, Montoya, Benavides, & Góngora	Evaluation of *Beauveria bassiana* (Ascomycota: Hypocreales) as a control of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) emerging from fallen, infested coffee berries on the ground	*Beauveria bassiana*	Biocontrol Science and Technology
14	2012	Manton, Hollingsworth, & Cabos	Potential of *Steinernema carpocapsae* (Rhabditida: Steinernematidae) against *Hypothenemus hampei* (Coleoptera: Curculionidae) in Hawai'i	*Steinernema carpocapsae*	Florida Entomologist
15	2013	Gonthier, Ennis, Philpott, Vandermeer, & Perfecto	Ants defend coffee from berry borer colonization	*Wasmannia auropunctata*	Biocontrol
16	2013	Infante, F.,Castillo, A., Pérez, J. & Vega, F.E.	Field-cage evaluation of the parasitoid *Phymastichus coffea* as a natural enemy of the coffee berry borer, *Hypothenemus hampei*	*Phymastichus coffea*	Biological Control
17	2013	Jiménez-Soto, Cruz-Rodríguez, Vandermeer, & Perfecto	*Hypothenemus hampei* (Coleoptera: Curculionidae) and its interactions with *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a shade coffee agroecosystem	Ants	Environmental Entomology

No.	Year	Authors	Tittle	Controller species	Journal
18	2013	Karp *et al.*	Forest bolsters bird abundance, pest control, and coffee yield	Birds	Environmental Entomology
19	2014	Trible & Carroll	Manipulating tropical fire ants to reduce the coffee berry borer	Ants displaced by *Solenopsis geminata*	Ecological Entomology
20	2015	J. L. Jaramillo, Montoya, Benavides, & Góngora B, 2015	*Beauveria bassiana* and *Metarhizium anisopliae* mix to control the coffee berry borer in soil fruits	*Beauveria bassiana*	Revista Colombiana de Entomología
21	2015	Morris, Vandermeer, & Perfecto	A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities	*Azteca sericeasur*	PLOS ONE
22	2016	Martínez-Salinas *et al.*	Bird functional diversity supports pest control services in a Costa Rican coffee farm using a Functional Diversity approach to study the effect of avian traits in *H. hampei* control.	Birds (gleaning birds)	Agriculture, Ecosystems, and Environment

Table 2. Success of CBB biocontrol by predators -ants and birds-. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1] Percentage of success compared with the treatment (without biocontrol agents) in the field. Percentages were estimated as [*1-(Treatment/Control)*100*] for variable I. For variables II, III and IV percentages were estimated as [*Control*100/Treatment*].

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	BIOCONTROL AGENT	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Ants	I. CBB mortality	Percentage of CBB removed from berries	Ants displaced by *S. geminata*	6	23	3.8	73,9%	Trible & Carroll	2014
	II. CBB abundance	CBB abundance in infested berries	Ants (Twig-nesting ants)	8.46	4.23	2.0	50,0%	Larsen & Philpott	2010
	III. Seed attack	Number of bored berries per branch	*Azteca sericeasur*	3.47-17.1	0.71-2.93	3.6-5.9	72,1 - 83,0%	Morris *et al.*	2015
		Number of CBB per branch	*Azteca instabilis*	4.048	2.14	1.9	47,1%	Gonthier *et al.*	2013
			Pheidole synanthropica	3.21	1.57	2.0	51,1%		
			Pseudomyrmex ejectus	3.856	2.32	1.7	39,8%		
			Pseudomyrmex simplex	4.075	2.836	1.4	30,4%		
			Tapinoma sp.	3.34	1.55	2.2	53,6%		
			Wasmannia auropunctata	4.069	2.169	1.9	46,7%		
		Percentage of infested berries	Ants	33.8	23.4	1.4	30,8%	Jiménez-Soto *et al.*	2013
			Azteca instabilis	33.8	21.5	1.6	36,4%		
			Pheidole synanthropica	33.8	18.4	1.8	45,6%		
	IV. CBB penetration length	Penetration depth into the berry (mm)	Ants	4	3.4	1.2	15,0%	Jiménez-Soto *et al.*	2013
			Pheidole synanthropica	4	2.7	1.5	32,5%		
Birds	II. CBB abundance	Percentage of CBB brood	Most of them warblers	0.34	0.18	1.9	48,3%	Kellerman *et al.*	2008
	III. Seed attack	Proportion of infested berries	Warblers mainly	2.92-9.37	1.33-5.98	1.6-2.2	36,2 - 54,6%	Karp *et al.*	2013
			Gleaning birds	6.08	5.72	1.1	6,0%	Martínes-Salinas *et al.*	2016
			Warblers mainly	0.14-0.15	0.08-0.09	1.7-1.8	41,0 - 45,6%	Kellerman *et al.*	2008
			Birds	0.19-0.43	0.10-0.21	1.8-3.2	44,2 - 68,5%	Johnson *et al.*	2010
	IV. CBB penetration length	Penetration depth into the berry (mm)	Birds (Warblers mainly)	5.48	3.87	1.4	29,4%	Kellerman *et al.*	2008

Table 3. Success of the entomopathogenic fungus *Beauveria bassiana* on CBB control. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1]= Percentage of success compared with the treatment (without biocontrol agents) in the field. Percentages were estimated as [*1-(Treatment/Control)*100*] for variable I. For variables II and III percentages were estimated as [*Control*100/Treatment*].

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	CONIDIAL SUSPENSION	STRAIN	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Beauveria bassiana	I. CBB mortality	Percentage of mycosis on CBB adults	$1x10^9$ conidia/tree	Bb 9205	6.0	19.3-21.7	3.6-4.9	68.9-72.4%	Bustillo *et al.*	1999
				Bb25	8.7	10.8	1.2	19.4%	De La Rosa *et al.*	2000
					0.0	27.3	NA	100.0%		
				Bb26	8.7	35.2	4.0	75.3%	De La Rosa *et al.*	2000
					4.7	35.5	7.6	86.8%		
					6.5	40.6	6.2	84.0%		
					6.1	32.9	5.4	81.5%		
					3.1	31.8	10.3	90.3%		
					0.9	15.3	17.0	94.1%		
					0.0	30.4	NA	100.0%		
					0.2	31.2	156	99.4%		
					0.0	33.9	NA	100.0%		
					0.0	28.9	NA	100.0%		
					0.0	28.4	NA	100.0%		
					0.0	21.0	NA	100.0%		
				Bb4	0.0	5.9	NA	100.0%	De La Rosa *et al.*	2000
					0.0	11.1	NA	100.0%		
					8.7	26.4	3.0	67.0%		
					4.7	19.8	4.2	76.3%		
					6.5	36.2	5.6	82.0%		
					6.1	33.5	5.5	81.8%		
					3.1	35.3	11.4	91.2%		
					0.9	28.8	32.0	96.9%		
					0.0	8.4	NA	100.0%		
					0.2	12.6	63.0	98.4%		
					0.0	15.0	NA	100.0%		
					0.0	13.0	NA	100.0%		
					0.0	6.6	NA	100.0%		
					0.0	3.5	NA	100.0%		
				Bb9205	10.7	53.6	5.0	80.0%	Vera *et al.*	2011
				Brocaril®	25.8	74.4	2.9	65.3%	Vera *et al.*	2011
					10.7	53.6	5.0	80.0%		
				Cenicafé mix (Bb9001+ Bb9024+ Bb9119)	25.8	61.1	2.4	57.8%	Vera *et al.*	2011
					10.7	75.5	7.0	85.8%		
		Percentage of CBB mortality	$1x10^6$ conidia/ml	Bb2	0.0	75.5-80.5	NA	100.0%	Haraprasad *et al.*	2001
					0.0	64.5-67.7	NA	100.0%		
					0.0	75.2-80.4	NA	100.0%		
					0.0	65.4-68.4	NA	100.0%		
					0.0	68.4-79.3	NA	100.0%		
					0.0	74.5-77.5	NA	100.0%		

Table 3. Continuation.

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	CONIDIAL SUSPENSION	STRAIN	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Beauveria bassiana	II. CBB abundance	Number of CBB per fruit	$1x10^9$ conidia/tree	Cenicafé mix (Bb9001+ Bb9024+ Bb9119)	10.2	6.5	1.6	36.3%	Jaramillo *et al.*	2015
	III. Seed attack	Percentage of CBB infestation	$1x10^9$ conidia/tree	Cenicafé mix (Bb9001+ Bb9024+ Bb9119)	12.5	10.3	1.2	17.6%	Jaramillo *et al.*	2015
		Percentage of CBB infestation	$1x10^6$ conidia/ml	Bb2	9.7	1.5	6.5	84.5%	Haraprasad *et al.*	2001
					20.5	1.8	11.4	91.2%		
					9.7	2.4	4.0	75.3%		
					19.3	1.6	12.1	91.7%		
					9.8	2.5	3.9	74.5%		
					18.3	1.8	10.2	90.2%		
					9.7	2.2	4.4	77.3%		
					15.3	1.3	11.8	91.5%		
					8.6	1.9	4.5	77.9%		
					14.3	1.4	10.2	90.2%		
					8.4	2.4	3.5	71.4%		
					13.1	1.5	8.7	88.5%		
					7.7	2.3	3.3	70.1%		
			$1x10E^9$ conidia/tree	Bb9205	27.7	18.8	1.5	32.1%	Vera *et al.*	2011
				Cenicafé mix (Bb9001+ Bb9024+ Bb9119)	15.0	9.2	1.6	38.7%		
					27.7	12.4	2.2	55.2%		

Table 4. Success of the entomopathogenic fungi *Metarhizium anisopliae,* on CBB mortality and coffee seed attack. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1]= Percentage of success compared with the treatment (without biocontrol agents) in the field. Percentages were estimated as [*1-(Treatment/Control)*100*] for variable I. For variable II percentages were estimated as [*Control*100/Treatment*].

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	CONIDIAL SUSPENSION	STRAIN	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Metarhizium anisopliae	I. CBB mortality	Percentage mycosis on adult CBB	$1x10^9$ conidia/ tree	Ma 9236	1.7	11.0	6.5	84.5%	Bustillo *et al.*	1999
					1.7	9.2	5.4	81.5%		
				Ma4	0.0	3.6	NA	100.0%	De La Rosa *et al.*	2000
					0.0	4.6	NA	100.0%		
					0.0	6.3	NA	100.0%		
					0.0	2.9	NA	100.0%		
					0.0	1.9	NA	100.0%		
					0.0	1.2	NA	100.0%		
					0.0	10.4	NA	100.0%		
					0.0	12.4	NA	100.0%		
					0.0	12.6	NA	100.0%		
					0.0	8.4	NA	100.0%		
					0.0	6.2	NA	100.0%		
					0.0	10.3	NA	100.0%		
					0.0	9.1	NA	100.0%		
					0.0	7.9	NA	100.0%		
					0.0	22.1	NA	100.0%		
					0.0	16.6	NA	100.0%		
				Ma5	0.0	1.4	NA	100.0%	De La Rosa *et al.*	2000
					0.0	0.5	NA	100.0%		
					0.0	5.4	NA	100.0%		
					0.0	7.1	NA	100.0%		
					0.0	11.4	NA	100.0%		
					0.0	9.0	NA	100.0%		
					0.0	7.7	NA	100.0%		
					0.0	7.9	NA	100.0%		
					0.0	7.9	NA	100.0%		
					0.0	7.6	NA	100.0%		
	III. Seed attack	Mean percentage of CBB infestation	$1x10^9$ conidia/tree	Ma9236	12.5	8.3	1.5	33.6%	Jaramillo *et al.*	2015

Table 5. Success of the entomopathogenic blend *Beauveria bassiana* + *Metarhizium anisopliae,* on CBB mortality and coffee seed attack. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1]= Percentage of success compared with the treatment (without biocontrol agents) in the field. For variables II and III percentages were estimated as [*Control*100/Treatment*].

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	CONIDIAL SUSPENSION	STRAIN	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Beauveria bassiana + *Metarhizium anisopliae*	II. CBB abundance	Mean CBB abundance per fruit	$1x10^9$ conidia/tree	Cenicafé mix+ Ma9236	10.2	7.1	1.4	30.4%	Jaramillo *et al.*	2015
	III. Seed attack	Mean percentage of CBB infestation	$1x10^9$ conidia/tree	Cenicafé mix+ Ma9236	12.5	6.6	1.9	47.2%	Jaramillo *et al.*	2015

Table 6. Success of the entomopathogenic nematodes *Heterorhabditis* sp and *Steinernema* spp., on CBB control. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1=] Percentage of success compared with the treatment (without biocontrol agents) in the field. Percentages were estimated as [*1-(Treatment/Control)*100*] for variable I. For variable II percentages were estimated as [*Control*100/Treatment*].

TAXON. GROUP	CONTROL CATEGORY	RESPONSE VARIABLE	CONIDIAL SUSPENSION	STRAIN	TREATMENT (BC exclusion)	CONTROL (presence of BC)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE (%)[1]	AUTHOR	YEAR
Heterorhabditis sp.	I. CBB mortality	Percentage of CBB mortality	Not mentioned	125.000 IJ/plate*	17.5	28.9	1.7	39.4%	Lara *et al.*	2004
				125.000 IJ/plate	6.1	78.5	12.9	92.2%		
				250.000 IJ/plate	6.1	82.0	13.4	92.6%		
				500.000 IJ/plate	6.1	53.2	8.7	88.5%		
	II. CBB abundance	Abundance of CBB life stages per fruit	Not mentioned	125.000 IJ/plate	13.0	3.5	3.7	73.1%	Lara *et al.*	2004
				250.000 IJ/plate	13.0	3.7	3.5	71.5%		
				500.000 IJ/plate	13.0	1.7	7.6	86.9%		
Steinernema carpocapsae	I. CBB mortality	Percentage of CBB larvae mortality	Millenium®	2500 IJ/mL**	0.0	17.1	NA	100%	Manton *et al.*	2012
		Percentage of CBB adults mortality	Millenium® + mulch	2500 IJ/mL	0.0	7.4	NA	100%	Manton *et al.*	2012
		Percentage of CBB larvae mortality	Millenium® + mulch	2500 IJ/mL	0.0	12.8	NA	100%		
Steinernema sp.	I. CBB mortality	Percentage of CBB mortality	Not mentioned	125.000 IJ/plate	6.1	71.3	11.7	91.4%	Lara *et al.*	2004
				250.000 IJ/plate	6.1	88.2	14.5	93.1%		
				250.00 IJ/plate	17.5	29.7	1.7	41.1%		
				500.000 IJ/plate	6.1	76.1	12.5	92.0%		
	II. CBB abundance	Abundance of CBB life stages per fruit	Not mentioned	125.000 IJ/plate	13.0	2.7	4.8	79.2%	Lara *et al.*	2004
				250.000 IJ/plate	13.0	2.7	4.8	79.2%		
				500.000 IJ/plate	13.0	0.2	65.0	98.5%		

Chapter 2 *Biocontrols of the coffee berry borer*

* Infectious Juveniles per 300mL water/coffee tree plate

** Infectious Juveniles per mL

Table 7. Success of the parasitoids *Cephalonomia stephanoderis* and *Phymastichus coffea* on CBB mortality, CBB abundance, coffee seed attack and seed dry weight. Only studies showing significant results between the treatment (exclusion of the biocontrol) and the control (presence of the biocontrol) are reported (BC= biocontrol agent). [1] Percentage of success compared with the treatment (without biocontrol agents) in the field. Percentages were estimated as [*1-(Treatment/Control)*100*] for variables I and V. For variables II, III and IV percentages were estimated as [*Control*100/Treatment*].

BIOCONTROL AGENT	CONTROL CATEGORY	RESPONSE VARIABLE	ABUNDANCE RATIO (PARASITOID: CBB)	TREATMENT (exclusion of NE)	CONTROL (presence of NE)	TIMES MORE EFFECTIVE THAN TREATMENT	CHANGE[1] (%)	AUTHOR	YEAR
Cephalonomia stephanoderis	I. CBB mortality	Number of dead CBB adults/fruit	5:1	0.11	0.49	4.5	77.6%	Aristizábal *et al.*	1998
				0.12	0.51	4.3	76.5%		
				0.12	0.34	2.8	64.7%		
				0.11	0.47	4.3	76.6%		
				0.12	0.53	4.4	77.4%		
				0.12	0.56	4.7	78.6%		
	II. CBB abundance	Number of CBB eggs	5:1	4.6	2.16	2.1	53.0%	Aristizábal *et al.*	1998
				5.45	1.7	3.2	68.8%		
				3.03	1.54	2.0	49.2%		
				4.6	2.22	2.1	51.7%		
				5.45	3.39	1.6	37.8%		
				3.03	2.26	1.3	25.4%		
		Number of CBB immature stages	5:1	10.15	2.69	3.8	73.5%	Aristizábal *et al.*	1998
				12.87	5.05	2.5	60.8%		
				14.94	5.59	2.7	62.6%		
				10.15	4.08	2.5	59.8%		
				12.87	7.29	1.8	43.4%		
				14.94	8.25	1.8	44.8%		
		Number of CBB larvae	5:1	5.21	0.65	8.0	87.5%	Aristizábal *et al.*	1998
				6.69	2.71	2.5	59.5%		
				8.79	3.58	2.5	59.3%		
				5.21	1.76	3.0	66.2%		
				6.69	3.21	2.1	52.0%		
				8.79	5.24	1.7	40.4%		
Phymastichus coffea	I. CBB mortality	Percentage of parasitism on CBB adults	1:10	0	86.7	NA	100.0%	Espinoza *et al.*	2009
				0	80.6	NA	100.0%		
				0	73	NA	100.0%		
				0	67.7	NA	100.0%		
				0	68.3	NA	100.0%		
	II. CBB abundance	Number of immature CBB stages per fruit	1:10	4.77	0.017	280.6	99.6%	Espinoza *et al.*	2009
				4.77	0.021	227.2	99.6%		
				4.77	0.077	62.0	98.4%		
				4.77	0.222	21.5	95.3%		
				4.77	0.395	12.1	91.7%		
	III. Seed attack	Percentage of infested berries	1:20	65.4	39.1	1.7	40.2%	Infante *et al.*	2013
				65.4	40.7	1.6	37.8%		
		Percentage of seed damage	1:10	36.6	6.59	5.6	82.0%	Infante *et al.*	2013
				36.6	7.543	4.9	79.4%		
				36.6	12.0	3.0	67.2%		
				36.6	12.0	3.0	67.2%		
				36.6	12.0	3.0	67.2%		
	V. Seed dry weight	Mean seed dry weight/ berry (g)	1:5	0.08	0.18	2.3	55.6%	Infante *et al.*	2013
			1:10	0.08	0.18	2.3	55.6%		
			1:15	0.08	0.13	1.6	38.5%		
			1:20	0.08	0.14	1.8	42.9%		
		Mean seed dry weight/branch (g)	1:5	3.2	10.2	3.2	68.6%	Infante *et al.*	2013
			1:10	3.2	9.9	3.1	67.7%		
			1:15	3.2	7.2	2.3	55.6%		
			1:20	3.2	6.9	2.2	53.6%		
			1:30	3.2	6.4	2.0	50.0%		

ANNEXES

Figures

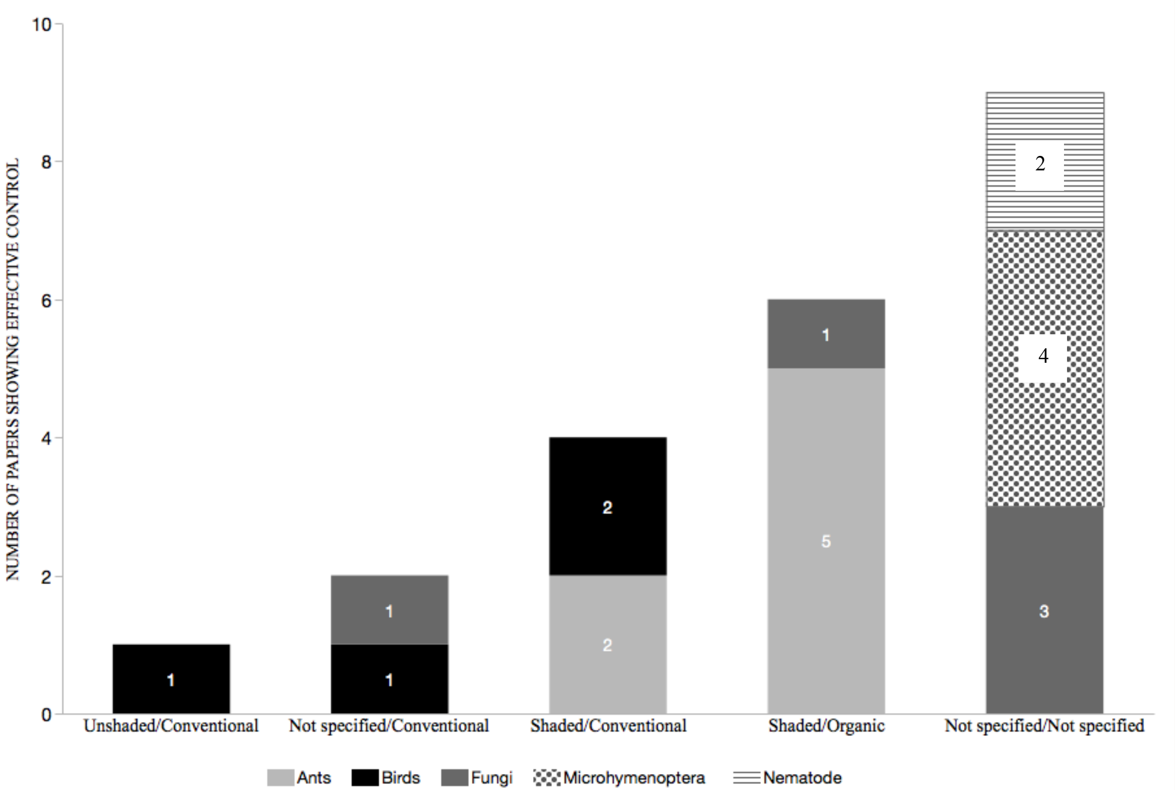

Figure A.1. The number of studies showing effective control (N= 22) by taxonomic groups under different types of management practices (presence of shade/ use of agrochemicals).

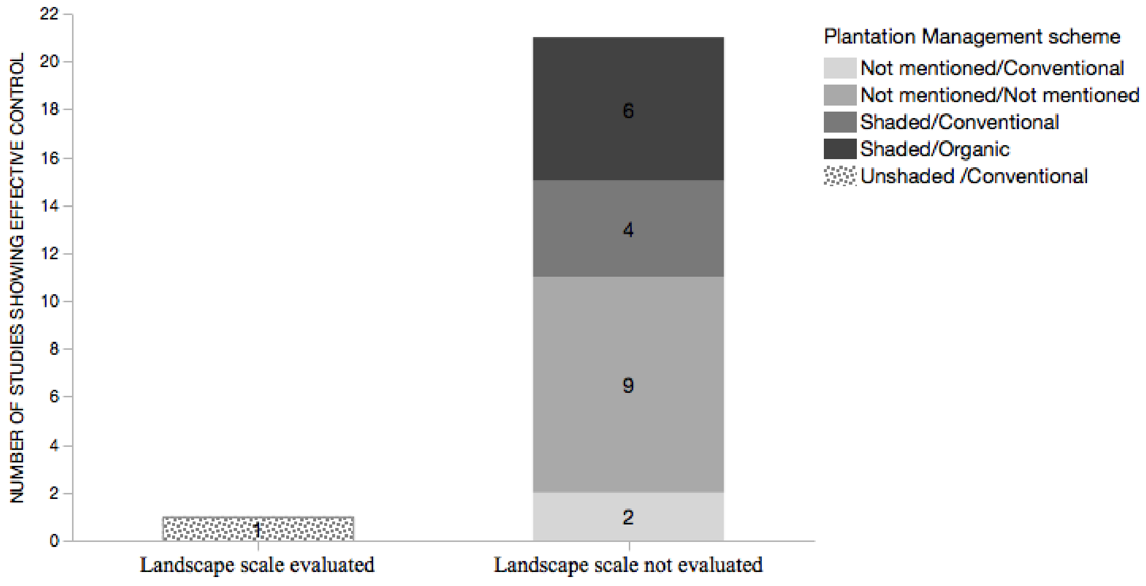

Figure A.2. The number of studies showing effective CBB control (N= 22, Table A.3) for each management scheme and how many of those included landscape scale variables.

Tables

Table A.1. Terms, phrases and strings (by searched category) used to search relevant literature in main engines, regarding biocontrol of the coffee berry borer CBB, *Hypotenemus hampei*.

Searched category	**Expanded terms**
1. Control of CBB by natural enemies	"*Hypothenemus hampei*" OR "coffee berry borer" OR "coffee bean beetle" AND "natural enem*" OR "parasit*" OR "predat*" OR "prey*" OR "pathogen*" OR "entomopathogen*" OR "competit*" AND "population size" OR "abundance" OR "crop damage" OR "survival" OR attack* OR "fruit damage" OR "mortality"
2. Laboratory vs. Field Efficiency	"*Hypothenemus hampei*" OR "coffee berry borer" OR "coffee bean beetle" AND "natural enem*" OR "parasit*" OR "predat*" OR "prey*" OR "pathogen*" OR "entomopathogen*" OR "competit*" AND "laborator*" OR "field" OR "*in situ" OR "ex situ"* AND "population size" OR "abundance" OR "crop damage" OR "survival" OR attack* OR "fruit damage" OR "mortality"
3. Local-scale management	"*Hypothenemus hampei*" OR "coffee berry borer" OR "coffee bean beetle" AND "organic" OR "shad*" OR "unshad*" OR "sun" OR "exposed" OR "tree*" OR "conventional" AND "population size" OR "abundance" OR "crop damage" OR "survival" OR attack* OR "fruit damage" OR "mortality" AND "ants" OR "natural enem*" OR "predat*" OR "prey*" OR "remov*"
4. Landscape-scale management	"*Hypothenemus hampei*" OR "coffee berry borer" OR "coffee bean beetle" AND "local" OR "landscape" OR "predictor" OR "driver" OR "land use" AND "population size" OR "abundance" OR "crop damage" OR "survival" OR attack* OR "fruit damage" OR "mortality" AND "ants" OR "natural enem*" OR "predat*" OR "prey*" OR "remov*"

Table A.2. List of 44 papers assessing direct effects of biological control agents on the CBB performance, including laboratory and field experiments.

Paper No.	Year	Author	Title	Experimental settings
1	1995	De La Rosa-Reyes, W., Godinez-Aguilar, J.L., Alatorre-Rosas, R.,	Biological activity of five strains of *Metarhizium anisopliae*, upon the coffee berry borer *Hypothenemus hampei* Col.: Scolytidae	Laboratory
2	1996	Castillo, A., Marbán-Mendoza, N.,	Laboratory evaluation of Steinernematid and Heterorhabditid nematodes for biological control of the coffee berry borer, *Hypothenemus hampei* Ferr	Laboratory
3	1996	Varela, A., Morales, E.,	Characterization of some *Beauveria bassiana* isolates and their virulence toward the coffee berry borer *Hypothenemus hampei*	Laboratory
4	1997	De la Rosa, W; Alatorre, R; Trujillo, J; Barrera, JF	Virulence of *Beauveria bassiana* (Deuteromycetes) strains against the coffee berry borer Coleoptera: Scolytidae	Laboratory
5	1998	Aristizábal, L.F.; Bustillo, A.E., Baker, P. S.; Orozco, J. H. & Chaves, B.	Depredatory effects of the parasitoid *Cephalonomia stephanoderis* on the immatures stages of *Hypothenemus hampei* in field conditions	Field
6	1999	Bustillo, A.E., Bernal, M.G., Benavides, P., Chaves, B.,	Dynamics of *Beauveria bassiana* and *Metarhizium anisopliae* infecting *Hypothenemus hampei* Coleoptera: Scolytidae populations emerging from fallen coffee berries	Field
7	2000	De La Rosa, W., Alatorre, R., Barrera, J.F., Toriello, C.,	Effect of *Beauveria bassiana* and *Metarhizium anisopliae* (Deuteromycetes) upon the coffee berry borer (Coleoptera: Scolytidae) under field conditions	Field
8	2001	Haraprasad, N., Niranjana, S.R., Prakash, H.S., Shetty, H.S., Wahab, S.	*Beauveria bassiana* - A potential mycopesticide for the efficient control of coffee berry borer, *Hypothenemus hampei* (Ferrari) in India	Field
9	2002	Damon, A; Valle, J	Comparison of two release techniques for the use of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae(, to control the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) in Soconusco, southeastern Mexico	Field
10	2002	Samuels, R.I., Pereira, R.C., Gava, C.A.T.,	Infection of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) by Brazilian isolates of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* (Deuteromycotina: Hyphomycetes)	Laboratory
11	2004	Castillo, A; Infante, F; Lopez, G; Trujillo, J; Kirkendall, LR; Vega, FE	Laboratory parasitism by *Phymastichus coffea* (Hymenoptera: Eulophidae) upon non-target bark beetles associated with coffee plantations	Laboratory
12	2004	Lara, J.C., López N. J.C. & Bustillo P., A.E.	Efecto de entomonematodos sobre poblaciones de la broca del cafe, *Hypothenemus hampei* (Coleoptera: Scolytidae), en frutos en el suelo.	Field
13	2005	Jaramillo, J., Bustillo, A.E., Montoya, E.C., Borgemeister, C.,	Biological control of the coffee berry borer *Hypothenemus hampei* Coleoptera: Curculionidae by *Phymastichus coffea* (Hymenoptera: Eulophidae) in Colombia	Field
14	2005	Neves, PMOJ; Hirose, E	*Beauveria bassiana* strains selection for biological control of the coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera: Scolytidae)	Laboratory
15	2005	Posada, F. J. & Vega, F.	A new method to evaluate the biocontrol potential of single spore isolates of fungal entomopathogens	Laboratory
16	2006	Cruz, L.P., Gaitan, A.L., Gongora, C.E.,	Exploiting the genetic diversity of *Beauveria bassiana* for improving the biological control of the coffee berry borer through the use of strain mixtures	Laboratory

Paper No.	Year	Author	Title	Experimental settings
17	2006	Perfecto, I & J. Vandermeer	The effect of an ant-hemipteran mutualism on the coffee berry borer *Hypothenemus hampei* in southern Mexico	Field
18	2007	Armbrecht, I; Gallego, MC	Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia	Laboratory and field
19	2007	Sánchez, Lourdes; Rodríguez, Mayra G	Potentialities of *Heterorhabditis bacteriophora* Poinar strain hc1 for the management of *Hypothenemus hampei* ferr. II. Compatibility with *Beauveria bassiana* (Balsamo) Vuilleimin and Endosulfán	Laboratory
20	2008	Kellermann, JL; Johnson, MD; Stercho, AM; Hackett, SC	Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms	Field
21	2008	Pava-Ripoll, M., Posada, F.J., Momen, B., Wang, C., St. Leger, R.,	Increased pathogenicity against coffee berry borer, *Hypothenemus hampei* Coleoptera: Curculionidae by *Metarhizium anisopliae* expressing the scorpion toxin AaIT gene	Laboratory
22	2008	Posada-Florez, Francisco J.	Production of *Beauveria bassiana* fungal spores on rice to control the coffee berry borer, *Hypothenemus hampei*, in Colombia	Laboratory
23	2009	Espinoza, J.C., Infante, F., Castillo, A., Pérez, J., Nieto, G., Pinson, E.P., Vega, F.E.,	The biology of Phymastichus coffea LaSalle Hymenoptera: Eulophidae under field conditions	Field
24	2009	Jaramillo, Juliana; Chabi-Olaye, Adenirin; Borgemeister, Christian; Kamonjo, Charles; Poehling, Hans-Michael; Vega, Fernando E.	Where to sample? Ecological implications of sampling strata in determining abundance and impact of natural enemies of the coffee berry borer, *Hypothenemus hampei*	Laboratory
25	2010	Jaramillo, J; Chapman, EG; Vega, FE; Harwood, JD	Molecular diagnosis of a previously unreported predator-prey association in coffee: *Karnyothrips flavipes* Jones (Thysanoptera: Phlaeothripidae) predation on the coffee berry borer	Laboratory
26	2010	Johnson, M. D.; Kellermann, J. L.; Stercho, A. M.	Pest reduction services by birds in shade and sun coffee in Jamaica	Field
27	2010	Larsen, A; Philpott, SM	Twig-Nesting Ants: The Hidden Predators of the Coffee Berry Borer in Chiapas, Mexico	Laboratory and field
28	2011	Pardee, Gabriella L.; Philpott, Stacy M.	Cascading Indirect Effects in a Coffee Agroecosystem: Effects of Parasitic Phorid Flies on Ants and the Coffee Berry Borer in a High-Shade and Low-Shade Habitat	Laboratory and field
29	2011	Vera, J.T., Montoya, E.C., Benavides, P., GÌ_ngora, C.E.,	Evaluation of *Beauveria bassiana* Ascomycota: Hypocreales as a control of the coffee berry borer *Hypothenemus hampei* Coleoptera: Curculionidae: Scolytinae emerging from fallen, infested coffee berries on the ground	Field
30	2012	Manton, JL; Hollingsworth, RG; Cabos, RYM	Potential of *Steinernema carpocapsae* (Rhabditida: Steinernematidae) against *Hypothenemus hampei* (Coleoptera: Curculionidae) in Hawai'i	Laboratory and field
31	2012	Philpott, Stacy M.; Pardee, Gabriella L.; Gonthier, David J.	Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity	Laboratory
32	2013	Gonthier, David J.; Ennis, Katherine K.; Philpott, Stacy M.; Vandermeer, John; Perfecto, Ivette	Ants defend coffee from berry borer colonization	Field

Paper No.	Year	Author	Title	Experimental settings
33	2013	Infante, Francisco; Castillo, Alfredo; Perez, Jeanneth; Vega, Fernando E.	Field-cage evaluation of the parasitoid *Phymastichus coffea* as a natural enemy of the coffee berry borer, *Hypothenemus hampei*	Field
34	2013	Jimenez-Soto, Esteli; Cruz-Rodriguez, Juan A.; Vandermeer, John; Perfecto, Ivette	*Hypothenemus hampei* (Coleoptera: Curculionidae) and its Interactions With *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a Shade Coffee Agroecosystem	Field
35	2013	Karp, Daniel S.; Mendenhall, Chase D.; Sandi, Randi Figueroa; Chaumont, Nicolas; Ehrlich, Paul R.; Hadly, Elizabeth A.; Daily, Gretchen C.	Forest bolsters bird abundance, pest control, and coffee yield	Field
36	2014	Trible, Waring; Carroll, Ron	Manipulating tropical fire ants to reduce the coffee berry borer	Field
37	2015	De la Mora, A.; Garcia-Ballinas, J. A.; Philpott, S. M.	Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico	Field
38	2015	Jaramillo, J.L., Montoya, E.C., Benavides, P., Góngora B, C.E.,	*Beauveria bassiana* and *Metarhizium anisopliae* mix to control the coffee berry borer in soil fruits	Laboratory and field
39	2015	Morris, Jonathan R.; Vandermeer, John; Perfecto, Ivette	A Keystone Ant Species Provides Robust Biological Control of the Coffee Berry Borer Under Varying Pest Densities	Field
40	2016	Follet et al.	Predation by flat bark beetles (Coleoptera: Silvanidae and Laemophloeidae) on coffee berry borer (Coleoptera: Curculionidae) in Hawaii coffee	Laboratory
41	2016	Geronimo-Torres, JDC; Torres-De-La-Cruz, M; Perez-De-La Cruz, M; De-La-Cruz-Perez, A; Ortiz-Garcia, CF; Cappello-Garcia, S	Characterization of native isolates of *Beauveria bassiana* and its pathogenicity to *Hypothenemus hampei*, in Tabasco, Mexico	Laboratory
42	2016	Martínes-Salinas et al.	Bird functional diversity supports pest control services in a Costa Rican coffee farm using a Functional Diversity approach to study the effect of avian traits in *H. hampei* control.	Field
43	2016	Morris, J.R. & I. Perfecto	Testing the potential for ant predation of immature coffee berry borer *Hypothenemus hampei* life stages	Laboratory
44	2017	Monagan IV, Morris JR, Davis Rabosky AR, Perfecto I, Vandermeer J.	Anoles lizards as biocontrol agents in mainland and island agroecosystems.	Laboratory

CHAPTER 3

Decrease of beta diversity, but not alpha diversity of ants in unshaded coffee plantations

Abstract

In agricultural landscapes, local land-use intensity and the surrounding landscape complexity moderate local species diversity. Ants are ubiquitous in tropical landscapes and are important biocontrol agents of the coffee berry borer (CBB), the main coffee pest worldwide. Intensification of coffee production and deforestation in the surrounding landscape may reduce ant diversity, yet, patterns in α and β diversity of ants in coffee landscapes remain poorly understood. Here, ants were sampled in four plots of three different land-use types along an agricultural intensification gradient (forest, shaded coffee, unshaded coffee) in a Neotropical coffee landscape. Specifically, we evaluated differences in α (bait and plot-level) and β (between baits and between plots) components of ant richness as well as the average habitat specificity of ant communities in response to land-use type and the percentage of surrounding forest. Additionally, we compared the abundance of ants with potential as CBB biocontrol agents among land-uses. Results showed that ant β diversity among plots was significantly reduced with management intensity, i.e. loss of shade cover. While the amount of forest border adjacent to coffee plantations did not affect α or β diversity, increasing forest border increased habitat specificity of ants in forest plots, and decreased specificity in unshaded coffee plantations. Abundance of effective and potential CBB biocontrols genera was two times higher in unshaded coffee. We conclude that maintaining forest at landscape scales enhanced β diversity and habitat specificity of ants in forests, but not in unshaded coffee. Loss of forest cover at landscape scales may led to biotic homogenization of ant communities. Hence, the landscape-wide ant richness, associated with a higher potential response diversity, as well as the high abundance of effective CBB antagonists in unshaded plantations, appeared to be important in terms of CBB biocontrol.

Keywords: diversity patterns, additive partitioning, natural enemies, *Hypothenemus hampei.*

Introduction

Coffee is one of the socio-economically most important cash crops worldwide and an important contributor to cash income for 14-25 million families of smallholders (Jha et al., 2014; Valencia et al. 2014). Coffee landscapes under traditional crop management (i.e. with high diversity of shade tres), are important for biodiversity conservation and for provision of ecosystem services like natural pest control (Moguel and Toledo, 1999; Tscharntke *et al.*, 2011; Jha *et al.*, 2014) as they harbor a high diversity of natural enemies (De Beenhouwer, Aerts and Honnay, 2013; Aristizábal, Bustillo and Arthurs, 2016). However, the transformation of traditionally managed coffee landscapes into simplified and intensively managed systems menace their potential for natural pest control. Therefore, it is highly relevant to understand the drivers of natural enemies in coffee landscapes and how they respond to management practices at different spatial scales (Tscharntke *et al.*, 2012)

Ants are suggested to act as successful biocontrol agents of the coffee berry borer (from now CBB), *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae). The CBB is the economically most important coffee pest worldwide (Vega, Infante and Johnson, 2015; Morris *et al.*, 2018). Ants significantly reduce infestation rates of coffee berries by the CBB, with infestation rates reduced by up to 83% compared to berries from which ants were experimentally excluded (Gonthier *et al.*, 2013; Jiménez-Soto *et al.*, 2013; Morris, Vandermeer and Perfecto, 2015). The abundance and diversity of ants in coffee agroecosystems responds to multiple conservation practices, including habitat diversification (Armbrecht and Perfecto, 2003; Philpott, Perfecto and Vandermeer, 2008a) and management intensity (Philpott, Perfecto and Vandermeer, 2006a, 2008a). Although ant diversity patterns in response to management intensity at the plot-scale (i.e. the farm) are well documented for coffee (Armbrecht, Rivera and Perfecto, 2005; Philpott, Perfecto and Vandermeer, 2006b; Teodoro *et al.*, 2010), the effects of management intensification at the landscape scale on ant diversity are less clear (but see De la Mora, Murnen & Philpott 2013; Zabala, Arango & Chacón de Ulloa 2013).

Processes determining total species richness in a landscape operate at several spatial scales. Hence, important drivers may be ignored if analyses focus only on the plot level (Gering and

Crist 2002, Clough et al. 2007) because most arthropod species experience their habitat at spatial scales beyond the plot level due to spillover across the crop–noncrop interface (Tscharntke *et al.*, 2007). However, little is known about the spatial components of ant richness in coffee landscapes (De la Mora et al., 2013) and how local land-use intensity (e.g. shaded vs. unshaded coffee plantations) and the complexity of the surrounding landscape (e.g. amount of forest border next to coffee plantations) shape ant diversity. (Gurr, Wratten and Barbosa, 2000; Begg *et al.*, 2017)

A widely used approach to the study of biodiversity patterns at landscape scales is the partitioning of the total species diversity within a landscape (gamma, γ) into local (alpha, α) and between land-uses components (beta, β) (Wagner, Wildi and Ewald, 2000; Tylianakis, Klein and Tscharntke, 2005; Diekötter, Billeter and Crist, 2008). Here, the contribution of α and β diversity to the regional diversity (γ) can be quantified using additive partitioning ($\gamma = \alpha + \beta$). The α diversity is the diversity at the smallest sampling unit and β diversity is the diversity that results from shifts in species community composition through species turnover between multiple sampling units (Veech, 2005; Clough *et al.*, 2007). Diversity partitioning can also be conducted at spatial hierarchies, so that β diversity can be calculated from small to large spatial scales. For example, high levels of β diversity may already be apparent at relatively local scales when measuring ant diversity at multiple localities within a given coffee plantation. In addition, species turnover between land-use types (e.g. between shaded and unshaded coffee plantations) may further promote β diversity at larger scales, and thus contribute to the total diversity (γ) in a landscape. In addition to allowing for diversity partitioning on an unlimited number of scales (Wagner, Wildi and Ewald, 2000) α, β and γ values are expressed in the same units (mean number of species) and consequently directly comparable (Veech *et al.*, 2002). This makes diversity partitioning a powerful tool to assess effects of agricultural management practices and landscape complexity on natural enemies such as ants in heterogeneous tropical landscapes (Clough et al. 2007).

Besides understanding diversity patterns, it is also relevant to assess the structure of natural enemies´ community and how it responds to local and landscape management factors. At local scales, the distribution and ecology of ants is strongly influenced by environmental stress and competition so that species identity and abundance are in part explained by a trade-off between temperature and dominance (Bestelmeyer, 2000; Yanoviak and Kaspari, 2000). For instance, ant communities in intensively managed coffee plots without trees that provide shade are strongly dominated by generalist ants and “hot-climate specialists” (Perfecto and Vandermeer, 1996). Therefore, ant species are generally expected to show specificity for particular land-use type, corresponding to management practices at local and landscape scales (Teodoro *et al.*, 2010; De la Mora, Murnen and Philpott, 2013). However, there are no studies assessing whether habitat specificity of ants also relates to landscape factors such us the proportion of forest surrounding coffee plantations.

This is the first study to analyze simultaneously the relative contribution of spatial scale and habitat management on ant species richness in a Neotropical coffee landscape. Specifically this study focuses on: 1) how α and β diversity components of coffee-foraging ants change among forest, shaded coffee and unshaded coffee, and 2) whether diversity patterns are furthermore affected by the amount of forest border surrounding the study plots. Additionally, 3) we evaluate how species specificity differs among the land use types and how it is affected by the amount of forest border. Finally, 4) we compare abundances of ant genera in categories of potential for CBB control as a function of habitat management.

Methods

Study area: The study was carried out in the Popayán Plateau (Department of Cauca, Colombia) in altitudes from 1574 to 1779 m.a.s.l. in southwestern Andes in Colombia, located between western and central mountain ranges (Ayerbe-Quiñones and Johnston-Gonzalez, 2010) (Figure S1). The municipalities sampled, La Rejoya and La Venta, display an agricultural mosaic dominated by small-farm holders (1–2 ha) combining mainly shaded and unshaded coffee plantations, cattle pastures, sugar cane, cassava, pine plantations and forest vegetation as fragmented patches, riparian forest or strips dividing or crossing the farms.

Plot selection and characterization. A total of 12 plots were selected: four forest, four shaded coffee plantations and four unshaded coffee plantations. The plots were similar in age (coffee plants about 3-4 years old), area (Mean=1.8; SD= ±1.1 ha), coffee variety (var. Colombia) and management practices, but differ in the percentage of forest surrounding the plots (Table S1). Percentage of bordering forest was estimated for each plot using ArcGIS software (10.2) over orthophotos provided by the Colombian Coffee Growers Federation. Additionally, for each plot we estimated plant structure variables distributed in three vertical strata, following Mas & Dietsch (2003) and Armbrecht (2003): 1) *Arboreal strata* (canopy cover, canopy height, tree richness, tree density), 2) *Coffee bushes strata* (coffee bushes density, coffee bushes height, epiphyte richness and epiphyte density) and 3) *Soil stratum* (litter depth) (Figure S2).

Ant sampling: The coffee-foraging ants (from now ants) may reduce fruit attacks by the CBB (Morris *et al.*, 2018). Ants were sampled in the above-mentioned twelve plots using tuna baits, following Philpott et al. (2008b), between July and September 2014. In each plot we set a grid of 7 x 7 for a total of 49 baits separated 10 m between each other (similar to Perfecto et al. 2003). Each bait consisted of approximately 3g of tuna (in oil) in a piece of bond paper (14x13cm), folded and fixed to the main stem of the coffee bush (in trees with a DBH > 8 cm in forest plots), at breast height (Figure 1). After two hours, all ant individuals visiting the baits were collected in ethanol (96%) for later quantification and identification in the laboratory. Individuals were identified to species or morpho-species level with the help of taxonomic keys (AntWeb: Ants of Bolton World Catalog, Fernández, 2003, www.evergreen.edu/ants) and compared with specimens in the Ant Reference Collection at the Entomology Museum of Universidad del Valle (Cali, Colombia). A dry reference ant collection was built up, as well as two replicate collections in alcohol. Details on ant captures can be seen on-line in Jiménez et al. (2016).

Statistical analysis: We used additive partitioning of species diversity (Lande, 1996) to partition ant species richness into components that reflect diversity at the level of ant baits, between baits, plot level and between plots of the same land-use type. Alpha diversity at bait level (α_{bait}) was defined as the mean number of species per bait and study plot. The spatial turnover in ant richness between ant baits (β_{bait}) was calculated for each plot and land-use type as the total species richness per plot minus the mean number of species per bait for that plot. Species turnover between plots (β_{plot}) of the same land-use type was calculated as the total species richness of that land-use type (sampled over all replicates) minus the number of species per plot of that land-use type. In summary, the total diversity of a land-use type was

$$\gamma = \alpha_{\text{bait}} + \beta_{\text{bait}} + \beta_{\text{plot}}$$

We then used linear regression to model the partitioned diversity in response to land-use type and the amount of forest border at each study plot, as well as the interaction between the two predictors. The interaction term was dropped from the model if not significant for model parsimony.

We also assessed the habitat specificity of each ant species among the studied land-use types, using a habitat specificity index introduced by Tylianakis et al. (2005). The habitat specificity index compares the observed distribution of species among study plots to an expected distribution if species distributed themselves randomly among all habitats proportionally to the relative abundance of all species in each land-use type (Tylianakis, Klein and Tscharntke, 2005). The expected number of individuals per species i for plot j was calculated as $E_{ij} = N_i \times P_j$, where N_i is the total number of individuals of species i across all land-uses and P_j is the proportion of all individuals of all sampled species (across all land-uses) that were found in plot j. For each species, we compared E_{ij} to the observed number of individuals of species in i in plot j (O_{ij}) to calculate its habitat specificity as specificity = $log10(\left[\frac{O_{ij}}{E_{ij}}\right] + 1)$. For modeling purposes, we calculated the mean habitat specificity across all species per study plot, and modeled this in response to land-use type and amount of forest border, as well as their two-way interaction.

Finally, for each land-use type we estimated the mean abundance of ant individuals per bait and percentage of bait occupation (i.e. number of baits where at least one individual was collected, divided by the total number of offered baits per plot). To analyze how land-use type affects abundances of ant genera known to be important for CBB control, we compared the mean ant abundance per bait, considering three categories according to the available kind of evidence on CBB control efficacy by ants (Escobar-Ramirez *et al.*, 2018; Morris *et al.*, 2018), as follows: 1) “Effective” include genera with species shown to be effective CBB controller (i.e. compared with a control) under field conditions (i.e., *Azteca, Pheidole, Pseudomyrmex, Solenopsis* and *Wasmannia,* according to Gonthier *et al.* 2013); 2) "Potential control" for other genera including species effective under laboratory conditions and species with anecdotal mentions about CBB predation under laboratory or field conditions (i.e. *Crematogaster, Linepithema, Ectatomma* and *Gnamptogenys*) (Armbrecht and Gallego, 2007; Vega, Infante and Johnson, 2015); and 3) "No evidence" category for genera for which published evidence on CBB control does not exist (i.e. *Atta, Brachymyrmex, Camponotus, Cephalotes, Dorymyrmex, Myrmelachista, Nesomyrmex* and *Nylanderia*). For these analyses we considered only the baits recording presence of at least one individual, and performed nonparametric multiple comparisons using Wilcoxon matched-pairs test method (JMP® software, version 13.0).

Results

In total, we sampled 17.288 individuals of 40 ant species (including also morphospecies) in 17 genera (Figure S5). Species accumulation curves indicated that, in all study plots, sampling was sufficient to capture the vast majority of ant species diversity (Figure S3). Among the five subfamilies identified, Myrmicinae showed the highest species richness with 19 species. *Linepithema* was the most abundant genus (38.1% of individuals), followed by *Solenopsis* (26.6%) and *Pheidole* (21.1%) (Figure S4). The forest showed the highest number of total species, followed by shaded and unshaded coffee (Figure 2). Further, the forest registered a higher number of exclusive species (14 out of 20) compared to shaded and unshaded coffee (5 and 6 species, respectively). Additionally, shaded and unshaded coffee shared more ant species among each other than with forest.

Plot characterization: As expected, forest exhibited the most complex plant structure in terms of higher litter depth, tree density, canopy cover, tree richness, epiphyte richness, and epiphyte density (Figure S6). On the one hand, the shaded coffee resembled some of the structural characteristics in the forest, such as the presence of epiphytes and high values of canopy cover, height and litter depth. Additionally, shaded-coffee presented a lower density of coffee bushes, and harbored a significant higher richness and density of epiphytes than unshaded coffee. On the other hand, unshaded coffee showed the most intensified and simplified system, almost deprived of arboreal stratum and epiphytes, a higher coffee density than in shaded coffee plots and the lowest litter depth.

Additive partitioning of ant species richness: Mean α diversity at bait level was 0.40 ± 0.06 (mean ± 1SE throughout) ant species in forest, which was not significantly different from shaded coffee (0.48 ± 0.25) or unshaded coffee plantations (0.79 ± 0.12) (Table 1). The amount of forest border next to the sampled forest fragment or coffee plantation did not affect α diversity at bait level (Figure 3a; Table 1). Similarly, neither β diversity between baits within each sampling plot (forest: 7.10 ± 1.27; shaded coffee: 6.27 ± 0.96; unshaded coffee: 7.21 ± 1.27) nor α diversity at plot level (forest: 7.50 ± 1.32; shaded coffee: 6.75 ± 1.18; unshaded coffee: 8.00 ± 1.23) significantly differed among land-use types or with variation in the amount of forest border (Figure 3a; Table 1). However, β diversity of ant species richness between plots within each land-use type was significantly higher in forest (14.50 ± 1.32) than in unshaded coffee plantations (10.00 ± 1.23), with β diversity in shaded coffee plantations ranging in-between (12.25 ± 1.18; Figure 3a+3b; Table 1). The interaction between land-use type and forest border was not significant in any of the models.

Habitat specificity of ant species: An interactive effect between land-use type and the amount of forest border explained the average habitat specificity of ant species across study plots (Table 2). Thus, we found that a higher amount of forest border resulted in increased average habitat specificity of ants in forest plots, whereas this effect was reversed for ant species in unshaded coffee plantations (Figure 4). This finding suggests that forest fragments harbored the highest number of ant species with comparatively high habitat specificity, particularly when more forested habitat was bordering close-by (also supported by the distribution of ant species among land-use types; Figure 2). On the contrary, the proportion of habitat specialists in unshaded coffee was lower and declined when more forested habitat surrounded the plantation. Overall, the average habitat specificity of ants was always lower than expected from an index value at which the observed ant species distributions matches those of the expected distribution, i.e. under the assumption that ants are distributed among land-use types in proportion to sample sizes (the index value when observed = expected distribution: log10 (1 + 1) = 0.301; dashed line in Figure 4).

Relative abundances of genera with potential as CBB controllers: In general, a higher average abundance of individuals per bait was found in unshaded coffee plantations, compared to shaded coffee and forest (113.1, p <0.0001), but similar in forest and shaded coffee (35.8 and 42.6, respectively, p = 0.6844), which was related with the total percentage of bait occupation per land-use type (70.9%, 37.2% and 35.2%, respectively). The mean abundance per bait of "effective" controllers of CBB was significantly higher in unshaded coffee, when compared to forest and to shaded coffee ($p<0.01$) (Table 3) (Figure 5). The same pattern was found for "potential" controllers of CBB. The most represented genera in the three land-use types were *Solenopsis, Pheidole* and *Linepithema* (Figures S3, S4). The species *Wasmannia auropunctata* was found exclusively in coffee plantations and appeared to be related to *Inga* spp. trees, the most frequent tree species in shaded coffee plantations.

Discussion

This is the first study to introduce the additive portioning of β diversity to understand spatial components of the density of ant species with potential as CBB biocontrol agents in a coffee landscape. Significant differences in ant species richness emerged at the landscape level (β_{plot}), meaning that species richness between plots within each land-use type (i.e. forest, shaded and unshaded coffee) was significantly higher in forest than in unshaded coffee plantations. The interaction between land-use type and forest border was not significant in any of the models. However, a higher amount of forest border resulted in increased average habitat specificity of ants in forest plots, but reduced habitat specificity for ant species in unshaded coffee plantations. Finally, in unshaded coffee plots the mean ant abundance per bait of "effective" and "potential" CBB controllers, was twice as high as in forest and shaded coffee.

Spatial partitioning of ant diversity: The β diversity contributed to the largest part of overall species richness (>95%) in the coffee landscape. Our results support the hypothesis that enemy distribution in agricultural landscapes is determined mainly by β diversity among patches

(Tscharntke *et al.*, 2007). This pattern is similar to studies assessing ant richness changes along the landscape using more exhaustive sampling methods in non-cropped ecosystems, where β diversity greatly contributed to gamma diversity at intermediate and larger spatial scales (Campos *et al.*, 2011; Pacheco and Vasconcelos, 2012; Marques and Schoereder, 2013; Schmidt *et al.*, 2017). Our results suggest that heterogeneity between the plots could be determining ant species turnover in the studied area, representing the 35% of the total β diversity (Wagner, Wildi and Ewald, 2000). High species turnover, determining the species pool at regional scales, is likely to explain β_{plot} richness, as has been suggested for different taxa in agricultural landscapes, including herbs and grasses, surface-dwelling arthropods, butterflies and social insects like bees (Wagner et al. 2000, Roschewitz et al. 2005, Clough et al. 2007, Ribeiro et al. 2008). High values of β diversity are expected in heterogeneous and highly fragmented landscapes where the overall species richness may be the result of dissimilarity in the composition of the species assemblages of the different plots that make up the landscape (Lande, 1996; Harrison, 1997; Pineda and Halffter, 2004). Low dispersal rates, in addition to sampling artifacts (i.e. low sampling effort) may affect β diversity estimations and therefore, biologically relevant conclusions (Chandy, Gibson and Robertson, 2006; Crist and Veech, 2006; Clough *et al.*, 2007). Here, species accumulation curves showed a satisfactory sampling efficacy (Figure S4); hence, dispersal limitation may explain the high β_{plot} diversity in this highly heterogeneous but fragmented landscape, where plots are isolated and ants are not using the bordering forest (i.e. amount of forested border did not affect α or β diversity) to disperse across the landscape. This finding may have important conservation implications regarding the permeability of the habitats.

Effects of land-use type on ant diversity: The α diversity of ants at plot level was not different among the land-use types, so we assume that despite of the strong structural differences among forest and shaded and unshaded coffee plots, this group of ants is apparently little affected by local habitat characteristics. Similar results were found by Perfecto & Snelling (1995) for ants foraging on coffee bushes in Mexico. However, in the present study, the β diversity between plots was higher in the forest than in unshaded coffee (with shaded coffee being intermediate), indicating an effect of the land-use type on species turnover. This means, our results suggest that differences on ant diversity (with a high potential as CBB biocontrols) between land-use types are apparently emerging only at the landscape scale (Duelli, 1997; Wagner, Wildi and Ewald, 2000).

Forest fragments supported the highest overall species richness and the highest number of exclusive species, highlighting the importance of better-preserved habitats as source of species that can act as CBB controllers for the coffee crops. Additionally, results suggest that unshaded coffee plots were more similar in species composition across space than those located in the forest, similar to the general pattern reported by Tscharntke et al. (2007) for managed systems when compared to natural habitats. In spite of more similar community composition, unshaded coffee plots shared 11 species (out of 22) with shaded coffee and five species with plots in the forest.

Habitat specificity of ant species: In general, ant species of forest plots showed a higher habitat specificity, compared with coffee plantations. However, overall we found a lower habitat specificity of ants compared to expected statistical value used here. This result is similar to Tylianakis et al. (2005) who also found low habitat specificity of Hymenoptera in a coffee landscape in Ecuador, which decreased with increasing habitat disturbance. The lack of habitat specificity might be explained by the fact we used tuna baits to catch coffee-foraging ants. Tuna attracted several competitively dominant ants (i.e. *Linepithema* spp., *Pheidole* spp, *Solenopsis* spp, *Wasmannia auropunctata*) (Perfecto and Vandermeer, 1996; Philpott, Perfecto and Vandermeer, 2006a) that might be able to displace specialized predator species foraging on the bait.

Our results showed that in unshaded coffee plots, species-specificity decreased as the proportion of forest border increased. A higher amount of forested area around unshaded coffee was related to a reduction in the abundance of some species (like the very abundant *Linepithema neotropicum* and *Linepithema* sp1), while other species (i.e. *Solenopsis* sp.1) showed the opposite trend. This result suggest that apparently, an increase in the amount of forest bordering unshaded coffee plantations may upturn the movement of ant species between these two land-use types. This assumption highlights the importance of preserving forest to increase biodiversity in coffee landscapes that in turn can enhance ecosystem services such as CBB biological control (Perfecto and Vandermeer, 2002; Tscharntke *et al.*, 2005)

Abundance of ant genera with potential as CBB controllers: highest abundance of effective CBB controllers was found in unshaded coffee plantations. This result can be explained by the fact that the few species known to be effective biocontrols agents , belong to genera that are known to be dominant ant species in our unshaded coffee plantations (i.e. *Solenopsis* spp, *Pheidole* spp, and *Linepithema* spp). Dominant species usually display aggressive behavior against herbivores in the coffee plants they forage, suggesting that unshaded coffee creates conditions that favor effective CBB controllers. However the specific species should be carefully analyzed, as it is known *Pheidole* is a hyperdiverse genus, as well as *Solenopsis* (Wilson, 2003), including species able to provide ecosystem services like CBB biocontrol like *P. synantropica;* (Jiménez-Soto *et al.*, 2013) but also disservices like an increment in mealybug densities (.i.e. *Wasmannia auropunctata* and *Linepithema* spp; (Espadaler and Muller, 2012). Hence it is still necessary to test (as was not tested here) whether higher abundances of ants, here defined as effective CBB controls, are in fact reducing this pest.

Implications for conservation management: By analyzing patterns of β diversity, mechanisms that explain the assembly of natural enemies in coffee agroecosystems can be proposed. For instance, this study demonstrates that forests enhance ant species turnover (and richness) at the coffee landscape scale, through increasing β diversity between plots. This is in line with Tscharntke et al. (2007) who concluded that diversity needed for conservation biological control may occur where patch heterogeneity at larger spatial scales is high.

Our results also suggest that increasing the proportion of forested border might help to reduce the strong habitat specificity of dominant hot-climate specialist ants in intensively managed systems like unshaded coffee plantations, stressing the importance of natural habitat for a spillover of diverse enemies into coffee plantations. Ant communities in unshaded coffee showed lowest species turnover and thus, were more similar throughout the landscape (defined as biotic homogenization by Gámez-Virués et al. 2015 and Karp et al. 2012).

In conclusion, our results demonstrate the importance to maintain or restore forests to keep high diversity of potential CBB natural enemies for Conservation Biological Control

(Tscharntke et al. 2007) in coffee landscapes (Tylianakis, Klein and Tscharntke, 2005). Loss of forest cover at landscape scales led to biotic homogenization of ant communities, while unshaded plantations still harbor higher abundance of ant genera that are known to be effective biocontrol agents. Hence, the landscape-wide ant richness, associated with higher potential response diversity, as well as the high abundance of most effective CBB antagonists in unshaded plantations appeared to be important in terms of biological CBB control.

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Figures

a b

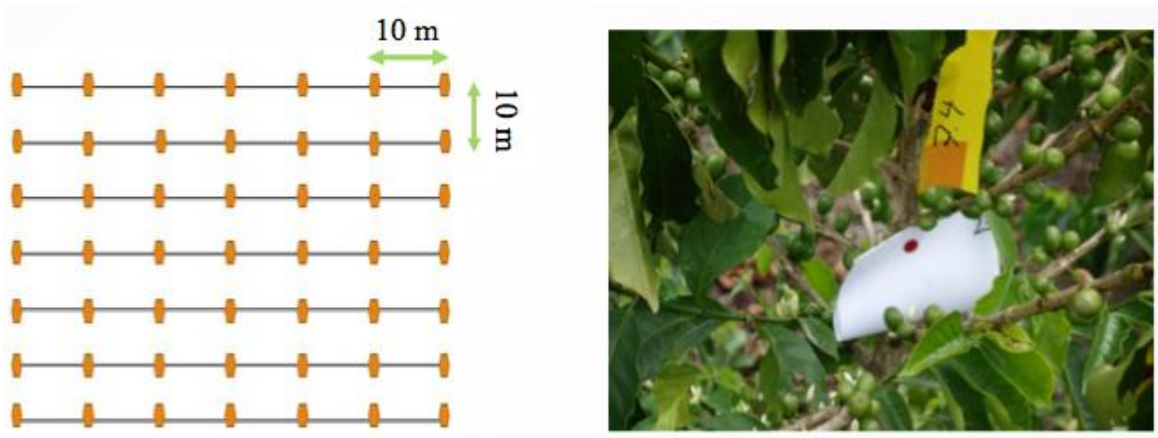

Figure 1. Distribution of ant sampling units in forest and coffee plots. A 7x7 sampling grid was placed in each plot (a), for a total of 49 tuna baits offered per sampled plot. Each arboreal tuna bait (b) was fixed in the main stem of a coffee bush at the breast height.

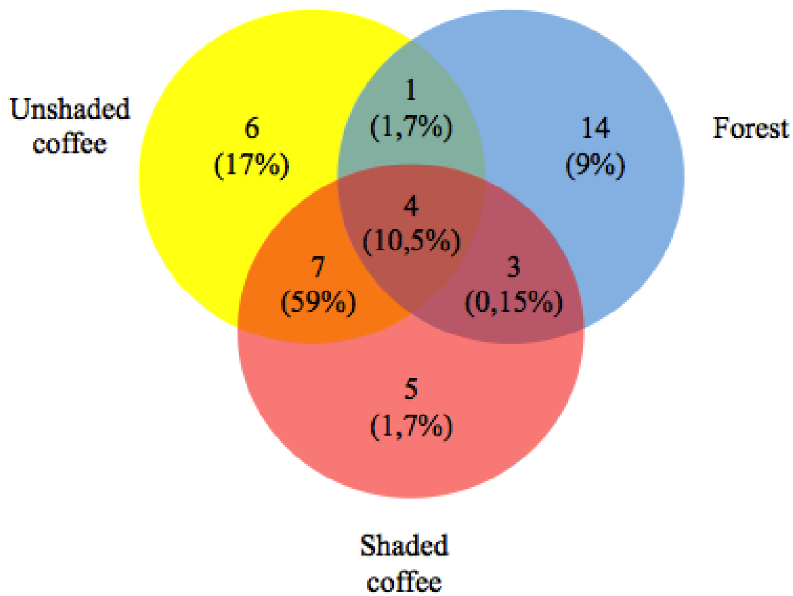

Figure 2. Number of species exclusive and shared among land-use types (i.e. 14 species were found exclusively in forest). In parenthesis, the abundance percentage of the species, regarding the total abundance in the sampling. For instance, seven species were common only to the shaded and unshaded coffee; all together, these seven species represented the 59% of the total abundance relative to total abundance of all species in the study.

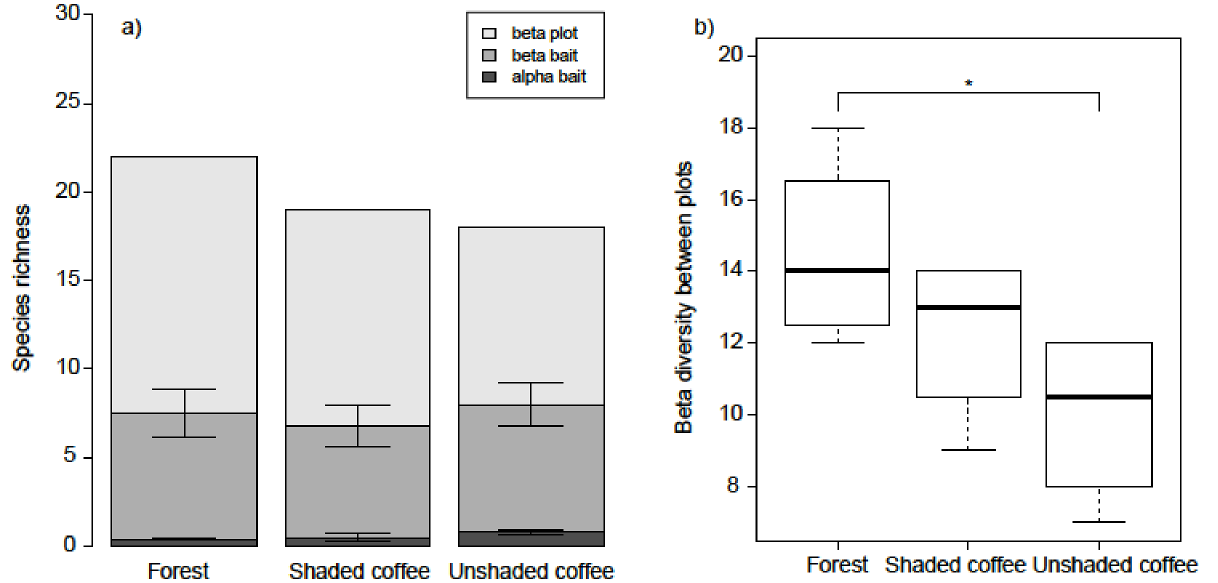

Figure 3**.** Additive diversity partitioning of a) ant species richness from bait to plot scale for each land-use type (means ± 1SE); b) Beta diversity between study plots is highest in forest and significantly ($p < 0.05$) reduced in unshaded coffee plantations.

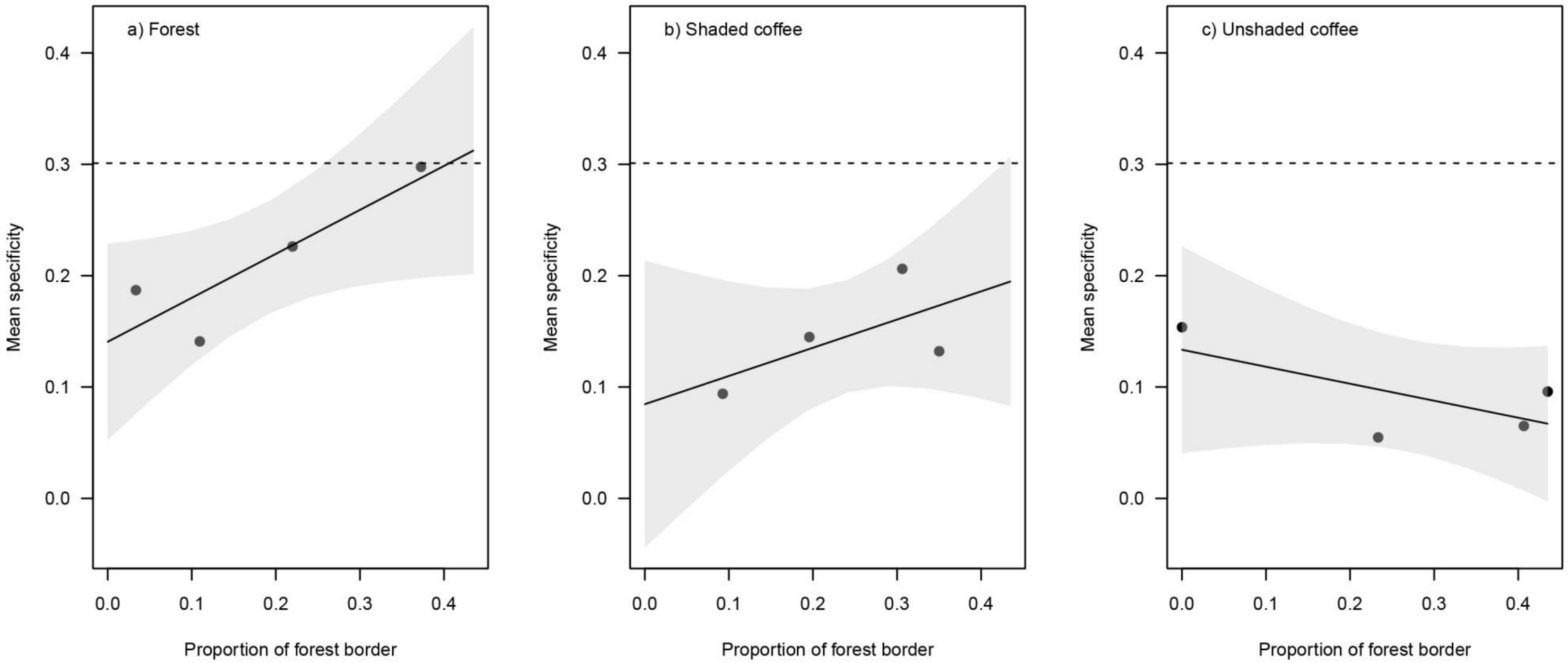

Figure 4. Interactive effects of land-use type and amount of forest border on the mean habitat specificity of ant species. The dashed line corresponds to the specificity value at which the observed distribution of species among land-uses matches those of an even distribution. Values below the line indicate lower than expected habitat specificity, values above the line higher than expected habitat specificity. Points: raw data; lines: predicted specificity; grey bands: 95 % confidence intervals.

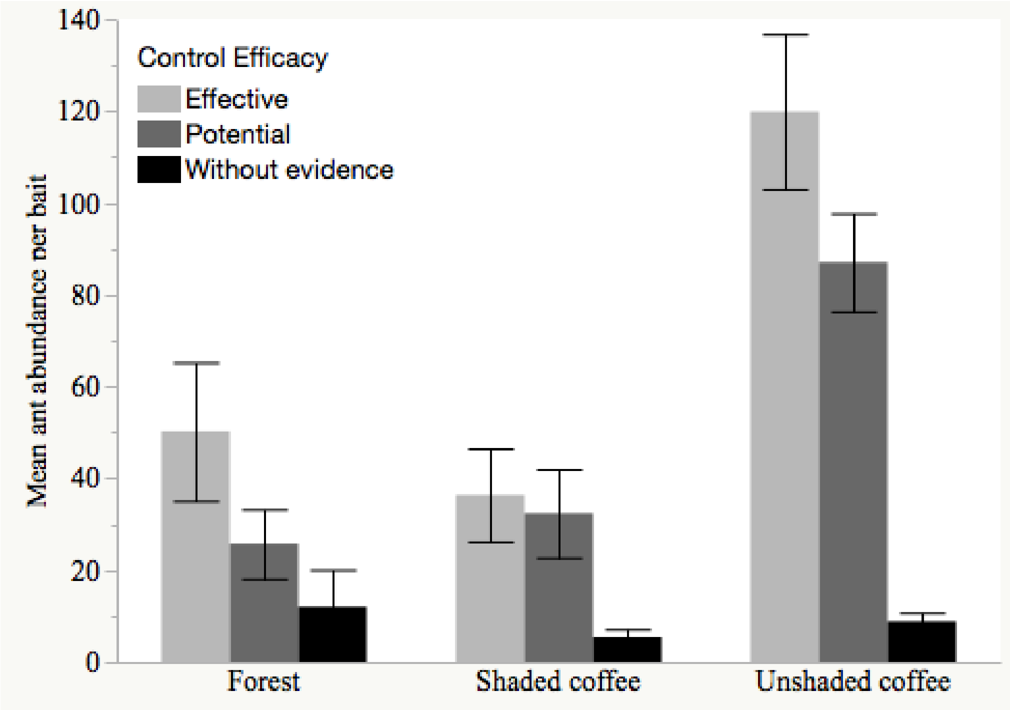

Figure 5. Mean bundance per bait (±SE) of ants in genus that include species known to be CBB biocontrols. Categories were set based on the strength of the evidence on control efficacy

Tables

Table 1. Additively partitioned diversity of ants in response to land-use type (forest, shaded coffee, unshaded coffee) and the amount of forest border at forest or plantation edges. Ant species richness was partitioned into spatial scales corresponding to (a) the mean number of species per bait within each plot, (b) the mean beta diversity between baits, (c) alpha diversity at plot level (n = 4 per land-use type) and (d) beta diversity between plots within land-uses. The interaction between land-use type and forest border was not significant in any of the models and thus omitted from these analyses.

	Estimate	**SE**	**t**	**p**
a) Alpha diversity at bait level				
(Intercept = Forest)	0.25	0.201	1.248	0.247
Shaded coffee	0.04	0.227	0.174	0.866
Unshaded coffee	0.325	0.231	1.403	0.198
Forest border	0.803	0.668	1.202	0.264
b) Beta diversity between baits within plots				
(Intercept = Forest)	7.321	1.572	4.657	0.002
Shaded coffee	–0.769	1.779	–0.432	0.677
Unshaded coffee	0.208	1.813	0.115	0.911
Forest border	–1.192	5.236	–0.228	0.826
c) Alpha diversity at plot level				
(Intercept = Forest)	7.572	1.669	4.536	0.002
Shaded coffee	–0.730	1.889	–0.386	0.709
Unshaded coffee	0.533	1.925	0.277	0.789
Forest border	–0.389	5.559	–0.070	0.946
d) Beta diversity between plots within land-uses				
(Intercept = Forest)	14.429	1.669	8.644	<0.001
Shaded coffee	–2.270	1.889	–1.202	0.264
Unshaded coffee	–4.533	1.925	–2.355	0.046*
Forest border	0.389	5.559	0.07	0.946

Table 2. Mean habitat specificity of ant species in the study plots in response to land-use type and the amount of forest bordering the study plots.

	Estimate	**SE**	**t**	**p**
(Intercept = Forest)	0.141	0.036	3.901	0.008***
Forest border	0.395	0.161	2.452	0.05*
Shaded coffee	–0.056	0.064	–0.878	0.414
Unshaded coffee	–0.007	0.052	–0.136	0.896
Forest border × Shaded coffee	–0.141	0.261	–0.543	0.607
Forest border × Unshaded coffee	–0.547	0.2	–2.738	0.034*

Table 3. Results of nonparametric multiple paired comparisons for mean abundance per bait among the three land-use types, considering the different categories of evidence on efficacy of ant as CBB controllers (Wilcoxon test)

Land-use type comparisons	Effective		Potential		No evidence	
	z	*p*-value	z	*p*-value	z	*p*-value
Unshaded coffee/ Shaded coffee	3.552	0.0004*	4.062	<.0001*	0.877	0.381
Unshaded coffee/ Forest	2.611	0.0090*	4.549	<.0001*	1.352	0.176
Shaded coffee/ Forest	-0.866	0.3850	0.251	0.802	0.385	0.700

ANNEXES

Figures

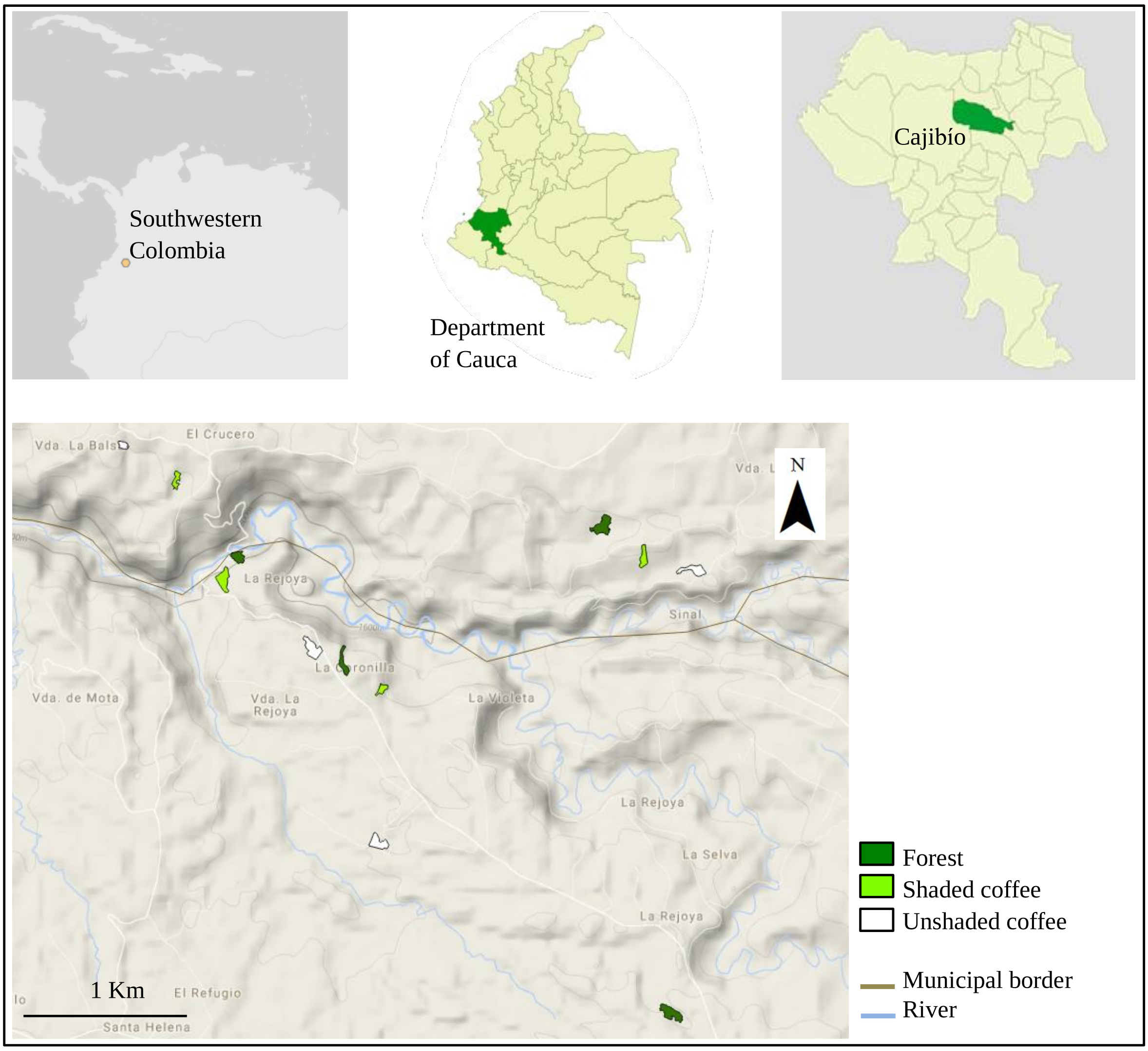

Figure S1. Location of the study site showing the twelve plots (4 forests, 4 shaded coffee and 4 unshaded coffee plots) where coffee foraging ants were sampled with tuna baits in Cajibío, Cauca (Southwestern Colombian coffee region).

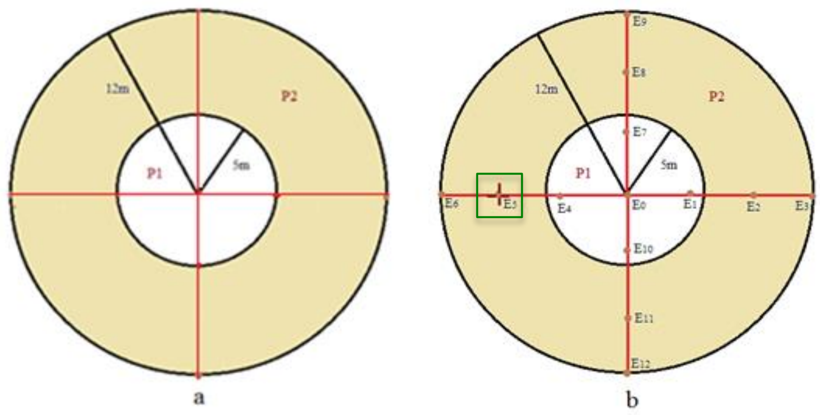

Figure S2. Graphical description of circular plots established to obtain vegetation-related variables at studied sites. In each coffee plantation, two circular plots (*a* and *b*) of 12m radius (P2) separated approximately 50m from each other, were established (following Armbrecht, 2003 and Mas and Dietsch, 2003) (for further details see Meneses-R. & Armbrecht 2018). In P2 of plots *a* and *b* denoted in the figure, height and DBH were measured for all shrubs (2,50≥ DBH≤ 8,10) and trees (DAP> 8,11 cm). Epiphytes density and diversity in trees were also recorded (up to 10m high). At the center of each P2 plot (12m radius) a sub plot (of 5m radius) was delimited (shown as P1) to quantify the number of coffee bushes and their respective height. Inside each P2 of plot *b*, thirteen stations ($E_{1,2,3,..n=13}$) were arranged along a Cartesian plane: station zero (E_0) was set in the center and six stations along each axis were separated each other by four meters. In each of these 13 stations leaf flitter depth and canopy cover was measured and recorded.

To calculate litter depth, a space was opened in the litter with a caliper until it touched firm ground, after which the thickness was measured. To calculate canopy cover, in each of the 13 stations, five cross measurements were made (GRS™ Densitometer): one in the center and four to one meter away from the center (as shown in plot *b*, E_5). The values were averaged at each station. Canopy height was measured in each of the 13 stations using a Haglöf EC II Electronic Clinometer®.

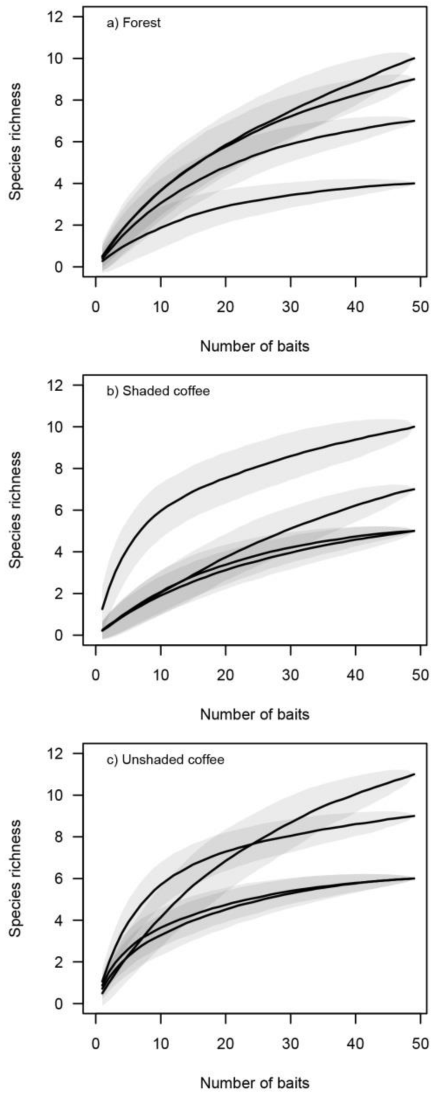

Figure S3. Species richness accumulation curves with increasing sampling intensity. Shown are accumulation curves for study plots in (a) forest, (b) shaded coffee and (c) unshaded coffee plantations. Solid lines indicate the expected number of species for a given number of ant baits, which is derived from random sub-sampling of the species data. Grey areas denote standard deviations of the means.

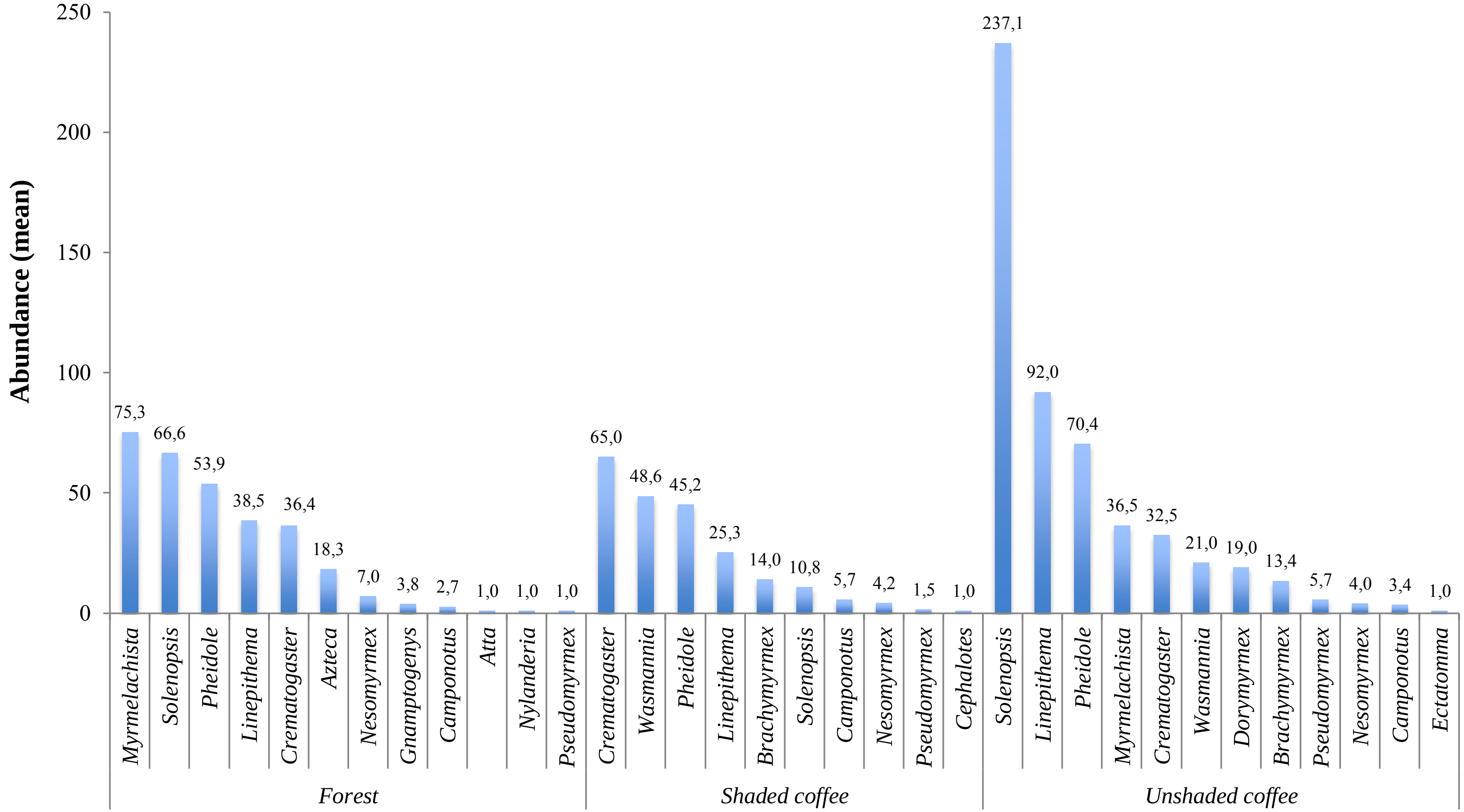

Figure S4. Mean abundance of ant genera recorded in the baits offered in i) forests and ii) shaded and iii) unshaded coffee plots.

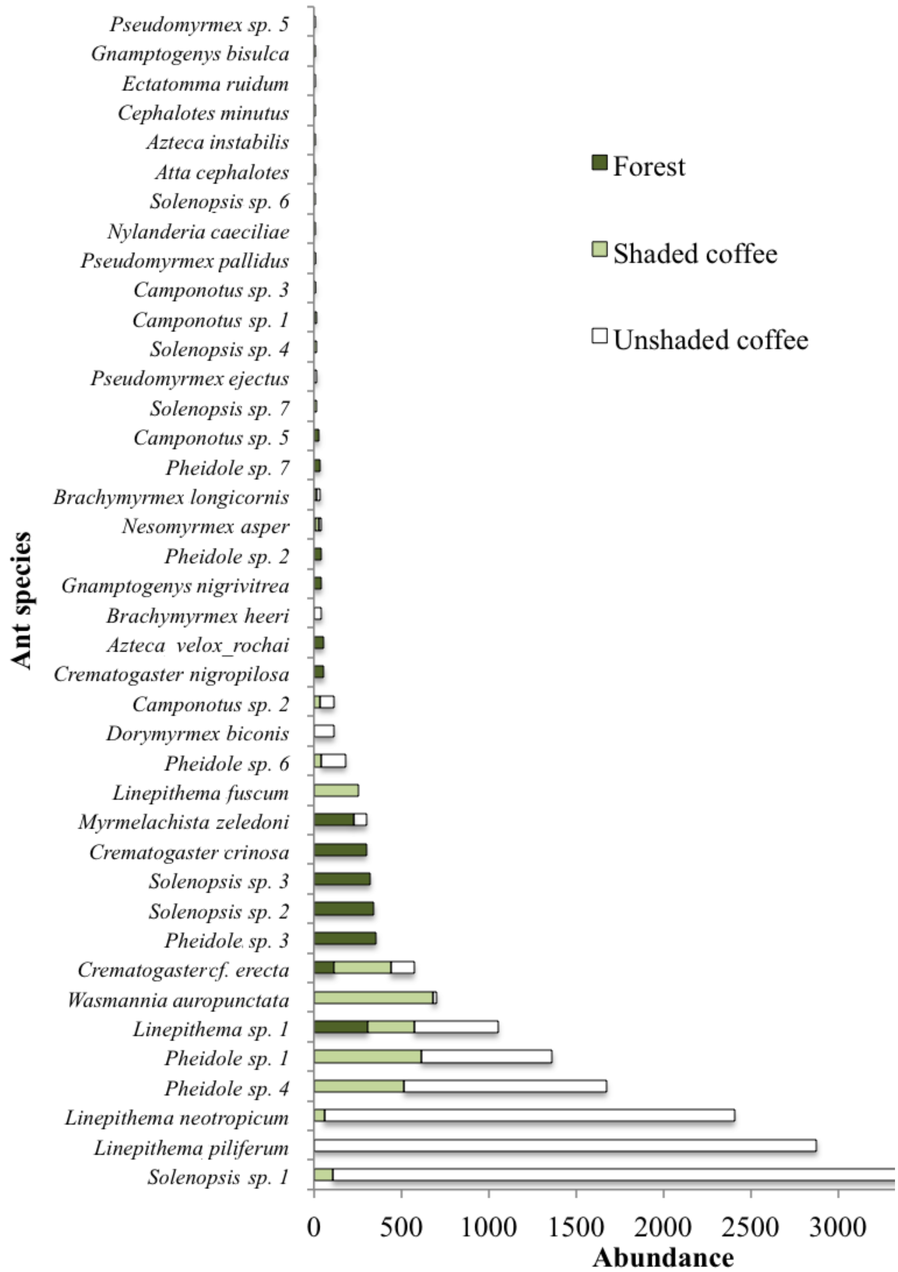

Figure S5. Total abundance of all the ant species found in the baits offered in the whole sampling

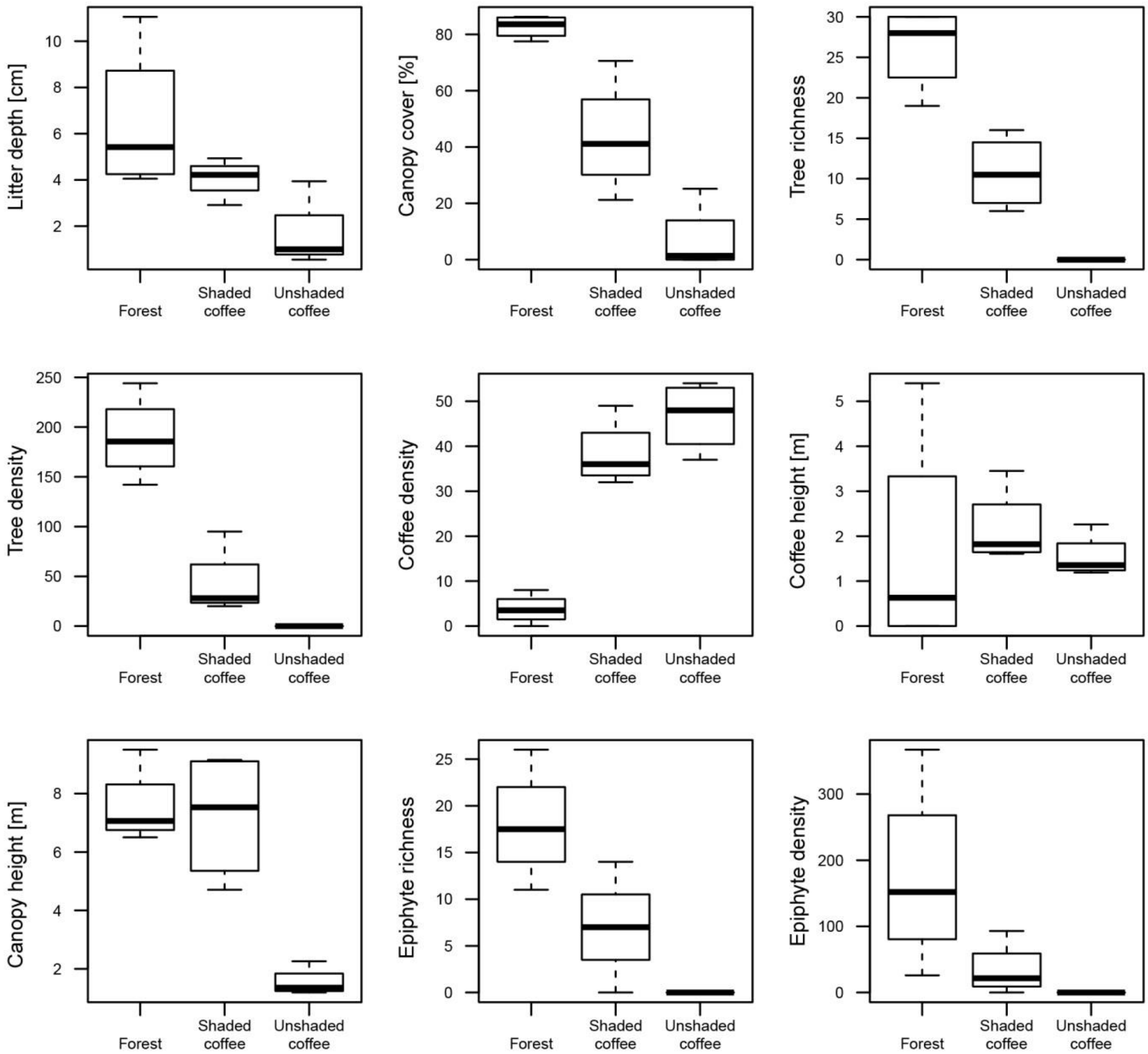

Figure S6. Structural variables describing heterogeneity of the selected land-use types.

Tables

Table S1. Location and description of the study plots where coffee foraging ants where sampled using tuna baits.

Land-use types	Farm	Elevation (m.a.s.l.)	Latitude N	Longitude W	Locality	Area (m^2)	Plot perimeter (m)	Border in Forest (m)	Border percentage in forest (%)
Forest	Normandía	1686	2°33'36.0"	76°35'59.8"	La Venta	31602.2	877.5	366.0	41.7
	Las Vegas	1574	2°33'29.2"	76°38'01.4"	La Rejoya	15725.1	510.6	112.5	22.0
	Unicauca	1779	2°31'01.1"	76°35'36.6"	La Rejoya	37667.6	1292.6	141.5	10.9
	Mirandé	1691	2°32'53.4"	76°37'26.5"	La Rejoya	16140.8	818.8	27.4	3.3
Shaded coffee	Normandía	1720	2°33'31.2"	76°35'47.1"	La Venta	37607.7	1190.9	419.0	35.2
	Don Jaime	1632	2°33'22.3"	76°38'05.1"	La Rejoya	29065.2	764.1	234.8	30.7
	Villa Alejandra	1690	2°32'45.7"	76°37'13.5"	La Rejoya	10172.2	456.0	89.7	19.7
	Los Guayabos	1721	2°33'57.2"	76°38'20.6"	La Venta	8310.0	574.5	53.7	9.3
Unshaded coffee	Santa Anita	1712	2°33'3.30"	76°37'37.7"	La Rejoya	21434.1	803.8	349.8	43.5
	La Cabaña	1715	2°33'25.0"	76°35'31.8"	La Venta	12110.8	784.8	321.2	40.9
	Don David	1758	2°31'53.8"	76°37'13.1"	La Rejoya	17930.9	694.9	163.2	23.5
	Medardo Peña	1731	2°34'4.90"	76°38'39.0"	La Venta	5916.0	374.5	0.0	0.0

CHAPTER 4

Landscape context, local management and ant presence determine infestation of coffee berry borers in Colombian coffee plantations.

Abstract

The coffee berry borer –CBB– is one of the most detrimental pests for coffee crops worldwide, causing significant annual losses in many tropical countries. Despite its economic importance, little research has been devoted to understand how local (i.e. presence of enemies such as ants, twigs and fruits on the ground enhancing enemies) and landscape-scale factors (plot area, plantation perimeter bordered by other crops) affect CBB. In order to fill this gap, we analyzed data from field assessments in a coffee landscape in Southwestern Colombia, one of the most productive coffee regions in the world. Specifically, we explored how 1) the exclusion of ants; 2) local factors (e.g. fruit and twig numbers, canopy cover); 3) landscape characteristics (plantation area, adjacent land use); and 4) interactions of local and landscape-scale significant variables, affected CBB infestation rates. Results showed that CBB infestation was higher (16.9 %) when ants were excluded. Additionally, higher numbers of twigs on the ground reduced CBB infestation, presumably due to the enhancement of ants. Surprisingly, tree cover and plantation perimeter bordering other crops were positively related to CBB infestation. In conclusion, the enhancement of ants, which may be done by increasing twig cover and possibly further measures, appeared to be the most important management to reduce CBB infestation, while the role of shade and bordering land-use needs further analysis.

Keywords: AIC, CBB biocontrol, coffee management, habitat complexity.

Introduction

Coffee production is one of the most significant cash crops on the globe and of particular importance for countries with a coffee-dependent economy (FAO, 2015). Among such countries, Colombia stands as the third coffee producing state reporting annual exportations values of ~2363 million USD (average for the last ten years, Federación Nacional de Cafeteros de Colombia, 2018). In spite of its notorious significance, coffee production in Colombia faces significant risks due mainly to biological threats (Aristizábal et al., 2016; Morris et al., 2018).

At the top of the list of known coffee pests is the coffee berry borer –CBB–, which represents more than $500 million dollars/year in economical losses to producing countries (Vega et al., 2015), Colombia included. Due to the negative relevance of this pest for coffee production in Colombia, many studies have tried to assess which factors enhance or diminish CBB fruit attacks in coffee plantations (Pérez et al., 2015; Vega et al., 2015), and the potential biocontrol agents that can reduce its noxious effects (Bustillo et al., 2002; Jaramillo et al., 2006)

As a result of the investigations testing best natural enemies of the CBB, ants (Hymenoptera: Formicidae) have been repeatedly highlighted as one of the most effective biocontrols for this insect pest (Morris et al., 2018, chapter 1). Results in this regard, have shown that not only the merely presence of ants help to reduce CBB prevalence but, also local factors (such as tree cover presence, leaf litter and twigs in the ground) may play a role to maintain ant richness and abundance (Armbrecht et al., 2006; Perfecto and Vandermeer, 1996), and thus, increase their potential predation rates. Additionally, there is still a debate on how these same local conditions are affecting or not CBB infestation rates towards coffee plants (Philpott et al., 2010; Soto-Pinto et al., 2002; Vega et al., 2015)

Likewise, a significant amount of recent literature highlights the importance of including landscape factors, such as forests surrounding coffee crops and plantations area, in the assessment of CBB infestation rates (Johnson et al., 2009; Jordani et al., 2015; Karp et al., 2013). Furthermore, specialized literature makes emphasis on understanding the interactions between local and landscape factors in order to explain, in a more comprehensive way, what is causing CBB to have higher negative effects on farms where coffee is the main crop (Avelino et al., 2012; De la Mora et al., 2015; Morris et al., 2018). Despite this notorious call by experts in this field, there are only a handful of investigations dealing explicitly with the interaction of local and landscape conditions and evaluating in the ground such dynamics for ants and the borer (De la Mora et al., 2015).

Understanding the role of ants, local, and landscape factors and more importantly, their interactions, will provide significant and essential data to inform management decisions regarding the CBB issue. Filling this important gap in our knowledge will directly aid to improve coffee agroecosystem configurations and enhance environmentally friendly practices in one of the most important areas for coffee production.

Here we present a novel approach and, to our knowledge, the first study to simultaneously analyze how CBB infestation rates in coffee fruits vary in relation to the presence of ants, and relevant local and landscape-scale variables related to the agricultural management of this crop. Specifically, we performed an exhaustive field assessment in a coffee landscape at Southwestern Colombia, in order to evaluate how CBB infestation rates are affected by 1) the exclusion of ants, 2) the variation of local factors (i.e. presence of tree cover, and accumulation in the ground of litter, twigs and coffee berries) and; 3) different landscape characteristics (i.e. plot area, the percentage of plots bordering other coffee crops, adjacent crops other than coffee and non-cropped area) that are usually recorded in the studied area. As a fourth and important specific objective of the present study, here we also present results using mathematical modeling and significant field data collection, that inform how the interactions among local and landscape scale variables may affect CBB infestation rates in coffee plantations.

Methods

Study area

This study was carried out in the municipality of Caldono (El Rosal village) in the Department of Cauca, southwestern Colombia (Figure 1), in an altitudinal range between 1400-1500 m above sea level and an average annual temperature of 21.5°C. The annual precipitation ranges around 2191 mm, usually showing a bimodal annual pattern with two high rain peaks in April - May, and October – November (Urrutia-Escobar and Armbrecht, 2013). The Department of Cauca is the seventh coffee producer in Colombia, recording 93.300 ha of its total extension dedicated to this product only (to December 2017), which represents 10,2% of the total cultivated area for the country (FNC, 2018a). Of the coffee cultivated land, close to half (45%) consists of unshaded coffee, and the other half (55%) represents coffee under total or partial shade (FNC, 2018b). In the last ten years, the region presents a strong trend to transform shaded into unshaded coffee. The area is predominantly agricultural, and other activities different than coffee plantation like production of sisal, cassava, pineapple and cattle ranching, are also common.

Testing ants effect over CBB infestation rates

To evaluate how CBB infestation rates were affected by ants (specific objective #1), an exclusion experiment was established within the study area. In order to perform such experiment, 10 coffee plantations (hereafter “plots”) presenting tree cover (“shade”) and 10 without such canopy (“unshaded”), were selected from a group of small farms located within a 2km radius in the Caldono-Colombian Cauca area. The fieldwork of the present study was initiated during the flowering season (floral buds and open flowers) on September 6 -12, 2016.

In each plot, five coffee bushes of similar age (2-3 years) and height (1,97 SD± 0,9 m) with a minimum of 10m apart, were chosen to perform the ant’s exclusion experiment (Figure 1). To mechanically perform such exclusion, five pairs of branches with a similar number of floral corsages were selected in each bush. In each branch pair, two different treatments were randomly assigned, on one side the treatment excluding ants; and second, a control allowing ants to access the branch. The branches assigned to the exclusion treatment were wrapped in the base with masking tape on which a sticky insect barrier (Tanglefoot®) was applied to avoid the entrance of ants (Figure 2). The ants present in these branches right after the application of the insect barrier were removed with a fine brush and the surrounding vegetation was pruned in order to avoid immediate ant arrivals. In the other hand, the control branches were labeled and left unmodified, so ants nesting near or in the bush and/or in the soil, were able to visit them. To ensure ants foraging activity at each coffee plant, an artificial substrate colonized by ants was attached to the lower part (40 cm from the ground) of the main stem of each experimental coffee bush. Each plot and the coffee bushes within them were geo referenced for later analyses (see “Local and landscape variables” section).

A total of 50 coffee bushes (5 bushes by 10 plots) in unshaded coffee plots and 50 coffee bushes in shaded coffee plots (i.e. 100 in total for this study) were installed, each of them with ten “experimental” branches: five assigned with the exclusion treatment and five assigned with the ant treatment (Figure 1).

Monthly inspections to experimental and control branches were conducted during the flowering period (September to November 2016), and from then on every week once the fruits began to grow at each plant, until the end of the harvest season in July 2017. During the inspections, ant colonization of the artificial substrates was verified. When substrate was abandoned, it was replaced with colonized substrates coming from a stock placed somewhere else (further from experimental influence area) within the same coffee plot. Additionally, the vegetation closely surrounding the excluded branches was pruned every one or two weeks, to eliminate natural branches for colonizing ants, and the insect barrier was removed and renewed with fresh product to exclude ants. At the weekly inspections, every single branch was observed for 30 seconds to verify ant activity. When present, ants in the branches with the exclusion treatment were removed. In models (and in Table 1) presented here, the derived variable from this section and used for the analyses is denoted as “Ant presence”.

Local and landscape scale variables

To evaluate the effect of local (at the bush/plant scale) and landscape (within the 2 km radius were “plots” were established in the study area) scale variables related to crop management and supposedly affecting CBB infestation rates, 10 variables were explicitly quantified in the 20 studied plots.

At the local or coffee bush scale, a 2x2 m quadrant was placed using each experimental coffee tree within the 20 plots as the center. In each quadrant, the number of hollow twigs (identified as potential nesting sites for the ants) were counted and recorded. Within the 2x2m quadrat, a smaller 1x1m square was established and the number of coffee fruits in the ground (considered as a source of CBB infestation), litter depth and litter volume were measured. In models these five variables are denoted as number of berries and twigs in the ground, leaf litter depth and volume, and presence of tree cover.

To calculate landscape scale variables, drone images obtained from three separate flights at 120 m from the ground (using a DJI Phantom 4, China) over the 2 km radius where the 20 plots were established, were used to assemble high-resolution mosaics of the study area (using Agisoft Photoscan software V 1.2.6). Mosaics were later imported to ArcMap (ESRI 2015, ArcGIS Release 10.4.1 Redlands, CA) and each georeferenced plot and coffee plant (used for ants exclusion and local scale variables) were geo located within the high-resolution images. Once plots and coffee trees were correctly referenced: first, the area and perimeter for each plot (20 in total) were measured (both variables defined as "Plot area" and "Plot perimeter" in the posterior analyses). Second, within the high-resolution mosaics the landscape heterogeneity for the plots and areas surrounding them, was classified in three main categories for the different agricultural units and characteristics repeating in the 2 km radius of the study site, in: i) coffee crops (shaded and unshaded coffee), ii) crops other than coffee, and iii) non-cropped areas (forest, riparian vegetation, abandoned plots, pastures, and family orchards).

After this landscape classification was performed, the length of study plots' perimeter in contact with: a) coffee plantations (denoted in models as "Plot perimeter bordering coffee"); b) with crops other than coffee ("Plot perimeter bordering other crops"), and c) other kind of non-agricultural areas ("Plot perimeter bordering non-cropped areas") were measured (using ArcGIS tools) for each experimental unit.

Response variable

Every week, during an 18 weeks period in the main harvest season for the region (specifically from March 6 to July 20, 2017), ripe fruits from each branch of the 100 coffee trees were hand-picked (resembling traditional collection methods) and later inspected for CBB attack. CBB inspection consisted in a visual confirmation of drilled holes in the berry by the herbivore, which has been referred as a positive attack (Jaramillo et al., 2005). The percentage of infested fruits was estimated as the number of attacked fruits over the total collected fruits, and later used for modeling approaches explained next.

Statistical analysis

All models explained below (Annex 1 contains details on coding) were assembled and run in R software (CRAN v. 3.5.0., Austria, 2018) using the lme4 package (Bates et al., 2011). Additionally, before assembling models, correlations between the different variables were tested to assess which factors should not be included in the different models presented below.

Ants presence importance to explain CBB infestation

We first analyzed whether ant exclusions affected infestation rates of coffee fruits, by fitting a linear-mixed effects model with the proportion of infested fruits in response to ant treatment (control vs. excluded). To account for the spatial hierarchy of our data, the model (and also next ones) included study plot, coffee tree and branch pair as random effects, with branch pair nested in coffee tree nested in study plot.

Local and landscape effects over CBB infestation rates

In order to assess specific objectives 2 and 3, a linear-mixed effects model was fitted for nine of the 10 local and landscape scale variables recorded as described in previous sections. “Plot perimeter” was not included in this analysis as it showed to be highly correlated with “Plot area” (Table 2). All the other nine variables were not correlated and thus, used in the analyses. Because we expected the effects tested in this section to be mainly indirectly mediated by changes in the biocontrol potential of ants (e.g., the number of twigs on the ground affects fruit infestation indirectly by changes in the biocontrol potential of ants), models that included landscape-scale variables only used data from branches where ants had not been excluded.

To inform how the interactions among local and landscape scale variables may affect CBB infestation rates, statistically significant variables in the above-mentioned linear-mixed effects model were chosen to perform an informative approach using the Akaike Information Criterion AIC (Burnham and Anderson, 1998). AIC was used as a goodness of fit measure to evaluate all candidate models (Table 3).

To perform this informative approach, a full interaction linear-mixed effects model was assembled and tested for each pair of combinations of the three tested variables. The AIC values were presented for each model in order to evaluate the best predictors for CBB infestation rates. AIC presents numerical information for each model that is used to contrast (using ΔAIC or the difference between each pair of models), which of them (separately or paired with other variable) was a better predictor to explain CBB infestations rates (Table 3). When ΔAIC falls between two units, each model within this range are considered good predictors of the response variable (Burnham and Anderson, 1998).

Results

Ant's effect over CBB infestation rates

We found strong evidence that ants act as biocontrol agents in the studied coffee system (Figure 2). The proportion of infested fruits on branches where ants had been excluded was significantly higher (11.2 %) as compared to neighboring branches (9.6 %) where ants had access to coffee fruits and thus potential pests ($ß = 0.016$; $SE = 0.005$; $P = 0.001$). Thus, the model predicted an absolute increase of 1.6 % infested fruits when ants were excluded, or a 16.9 % relative increase in fruit infestation as compared to untreated control branches. This strong ant effect was also found when contrasted with the other local variables (Table 1).

Local and landscape scale effects on CBB infestation rates

From the nine local and landscape variables used in the model to answer specific objective two (and using the subset data), only three variables, namely the number of twigs on the ground, the presence of tree cover and the plot perimeter bordering other crops, showed to be significant to explain CBB infestation rates. Specifically, a higher number of twigs on the ground significantly reduced the proportion of infested fruits (Figure 3a). Leaf litter volume had a marginally significant positive effect on infestation rates (Figure 3b). In addition, the presence of tree cover and larger plot perimeter sections bordering other crops, increased infestation rates (Table 2).

Local and landscape interactions affecting CBB infestation rates

Finally, when models including the different combinations for the three significant variables (from Table 2) and their respective AICs were contrasted (using ΔAIC), model testing the interaction between number of twigs in the ground and other crops perimeter, was the best estimator of CBB infestation rates (Table 3).

Discussion

The present study found evidence that ants are important biocontrol agents that reduce CBB infestations. Also, this investigation provides significant data regarding how local conditions (such as the presence of shade trees) and the physical environment below coffee trees (like the number of twigs) may also have an effect over coffee fruit attacks by CBB. In addition, to these important findings our analysis allowed us to evidence the apparent importance of both, local and landscape variables to explain coffee fruits attacks by CBB.

Similar to other investigations (Armbrecht and Gallego, 2007; Perfecto et al., 2014) this study highlights the ecological importance of ants for CBB control, one of the most noxious pests of coffee crops. This also means, that in order to maintain low CBB infestation rates, ant presence in coffee crops should be at least maintained or enhanced. Different authors (and also data from this investigation, Table 2) suggest that mechanical practices such us increasing (or at least leaving) leaf litter and hollow twigs right below the coffee trees, may enhance ant abundances by creating proper microhabitat conditions, and increasing food availability and nesting resources (Philpott and Foster, 2005). In theory and according to our experience, these practices to increase ant abundance in coffee crops can be easily implemented by local farmers, who in the long run may adopt them after seeing their benefits (Cowan and Gunby, 1996; Wilson and Tisdell, 2000). However, to see opposite results, refers to (Philpott et al., 2008).

Our data also suggest that, in addition to ants presence, other "local" factors such us tree cover over coffee crops are apparently of significant importance when explaining the CBB attacks. Although there is controversy about how shade can reduce the infestation of pests such as CBB (Aristizábal et al., 2016; Vega et al., 2015) our results suggest that the absence of shade would be helping to reduce the plague. Other investigations have shown that when ants are present and reproducing in unshaded coffee crops, that usually present lower food resources for these insects, they tend to increase predatory activity over coffee pest such as CBB (Symondson et al., 2002). This mechanism could be operating in the studied area and thus, explaining the observed result.

But on the other hand, it has been largely debated that shaded coffee plantations have a positive value over local and landscape biodiversity and also to enhance biological pest control services (Chaplin-Kramer et al., 2011; Perfecto and Vandermeer, 2015). Therefore, our results suggest that unshaded coffee areas should be surrounded by non-cropped areas such as forest, for example, that can maintain the biological services similarly to what occur in shaded coffee plantations, but with lower levels of CBB infestation.

It has been suggested how significant is the influence of the landscape configuration over pest-natural enemies interactions in important agricultural crops (Bianchi et al., 2006; Gámez-Virués et al., 2012; Rusch et al., 2016; Tscharntke et al., 2007). However, and as explained above, the number of investigations implicitly including the interactions between local and landscape variables that explain CBB infestation rates are still scarce. To fill this gap, this investigation presented for the first time (and for the studied area) a modeling approach showing how the interaction between the number of twigs on the ground, differential tree cover and how much of coffee plots perimeter is dominated by other crops, has an effect over CBB infestation rates. Derived from this result it can be speculated that in the studied area, coffee management should be focusing on maintaining plots that mainly records a high number of twigs in the ground and that are not surrounded extensively by crops different than coffee. The combination of both the manipulation of twigs in the ground and less perimeter of coffee plantations bordering non-cropped areas is apparently a better management combination than implementing each mechanism separately (from Table 3).

Unluckily, to rigorously test this assumption, experiments at proper landscape scales and testing for different configurations and sites need to be implemented. Such experiments can be logistically and economically difficult to perform, which, on the other hand, highlights the benefits of modelling approaches like the ones presented here.

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Figures

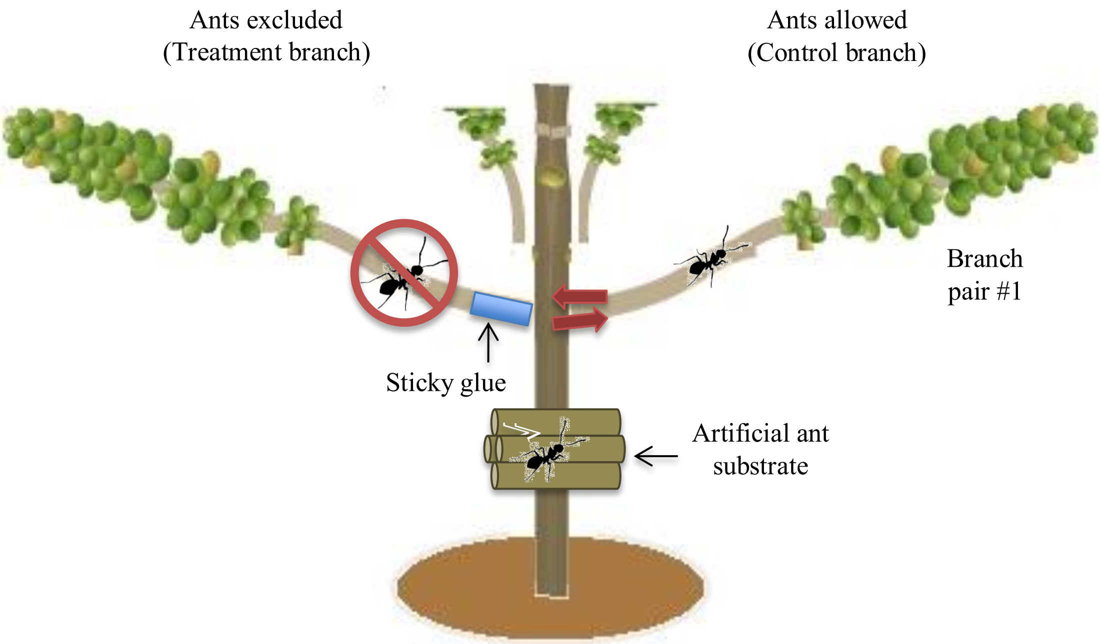

Figure 1. Illustration of the ant exclusion experiment performed in each coffee bush. Five pair of branches per tree were selected and randomly assigned for the control (ants allowed) and the experimental treatment (ants excluded). An artificial substrate colonized by ants, constructed with small and long paper tubes, was attached to the main stem of each coffee bush. Ant exclusions were performed in a total of 100 coffee bushes.

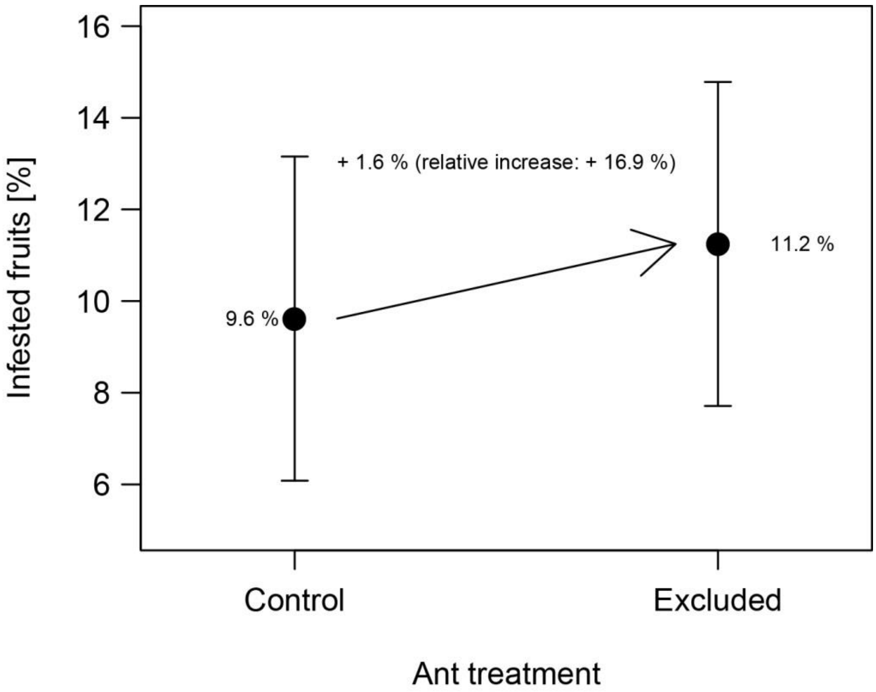

Figure 2. The percentage of infested coffee fruits increases when ants are excluded from coffee branches. Shown are model predictions from a linear-mixed effects model (mean ± 95% confidence intervals).

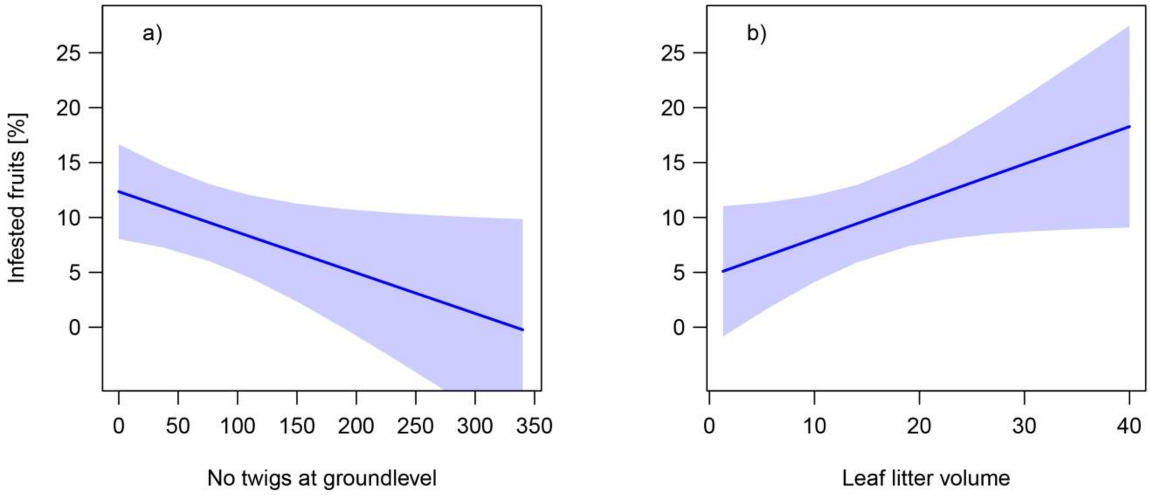

Figure 3. Local management affects fruit infestation of coffee trees**.** a) A greater number of twigs on the ground reduced the percentage of fruits infested by the CBB. b) Leaf litter volume has marginally significant positive effect on infestation rates.

Tables

Table 1. Effects of ants and considered local scale variables on the proportion of infested coffee fruits for this investigation.

Factor	Estimate	Std. Error	Z-value	Pr(>|z|)	
(Intercept)	0.070390	0.032580	2.161	0.03073	*
Ant presence	0.016170	0.005042	3.207	0.00134	**
Number of berries on the ground	0.000093	0.000059	1.57	0.11652	
Number of twigs on the ground	-0.000148	0.000172	-0.861	0.38932	
Leaf litter depth	-0.006816	0.006499	-1.049	0.2943	
Leaf litter volume	0.000893	0.001690	0.529	0.59714	
Tree cover	0.061790	0.038810	1.592	0.11135	

Table 2. Local and landscape variables affecting CBB infestation rates in a tropical coffee landscape, at South-western Colombia. For this model, only the infestation rates for control branches with ants were analyzed.

		Estimate	**SE**	**Z**	**P**
	(Intercept)	0.043070	0.075460	0.571	0.5681
LOCAL VARIABLES	Number of berries in the ground	0.000060	0.000060	1.002	0.3164
	Number of twigs in the ground	-0.000369	0.000180	-2.056	0.0398*
	Leaf litter depth	-0.009183	0.006681	-1.374	0.1693
	Leaf litter volume	0.002720	0.001753	1.552	0.1206
	Tree cover	0.082200	0.037200	2.21	0.0271*
LANDSCAPE VARIABLES	Plot area	-0.000007	0.000008	-0.856	0.3918
	Plot perimeter bordering coffee	-0.000264	0.000337	-0.783	0.4335
	Plot perimeter bordering other crops	0.001439	0.000646	2.227	0.0259*
	Plot perimeter bordering non-cropped areas	0.000322	0.000306	1.054	0.2919

Table 3. AIC values for the separate and combined effects of significant local and landscape variables predicting CBB infestation rates. The best model predicting CBB infestation rates was the one with lowest AIC value. The lowest the ΔAIC in a model, the better the model predicts CBB infestation rates. CBB infestation rates were better predicted by the interaction of the local and landscape variables than the single variables separately.

	Model	**Estimate**	**AIC**	**ΔAIC**
1	Number of twigs on the ground x Plot perimeter bordering other crops	-0.0000066	736.3	0
2	Number of twigs on the ground x Tree cover	-0.0006735	754.3	17.98
3	Tree cover x Plot perimeter bordering other crops	0.0010213	756.3	19.99
4	Number of twigs on the ground	-0.0002921	772.6	36.29
5	Plot perimeter bordering other crops	0.0006827	773.9	37.56
6	Tree cover	0.03404	781.5	45.13

ANNEXES

Figures

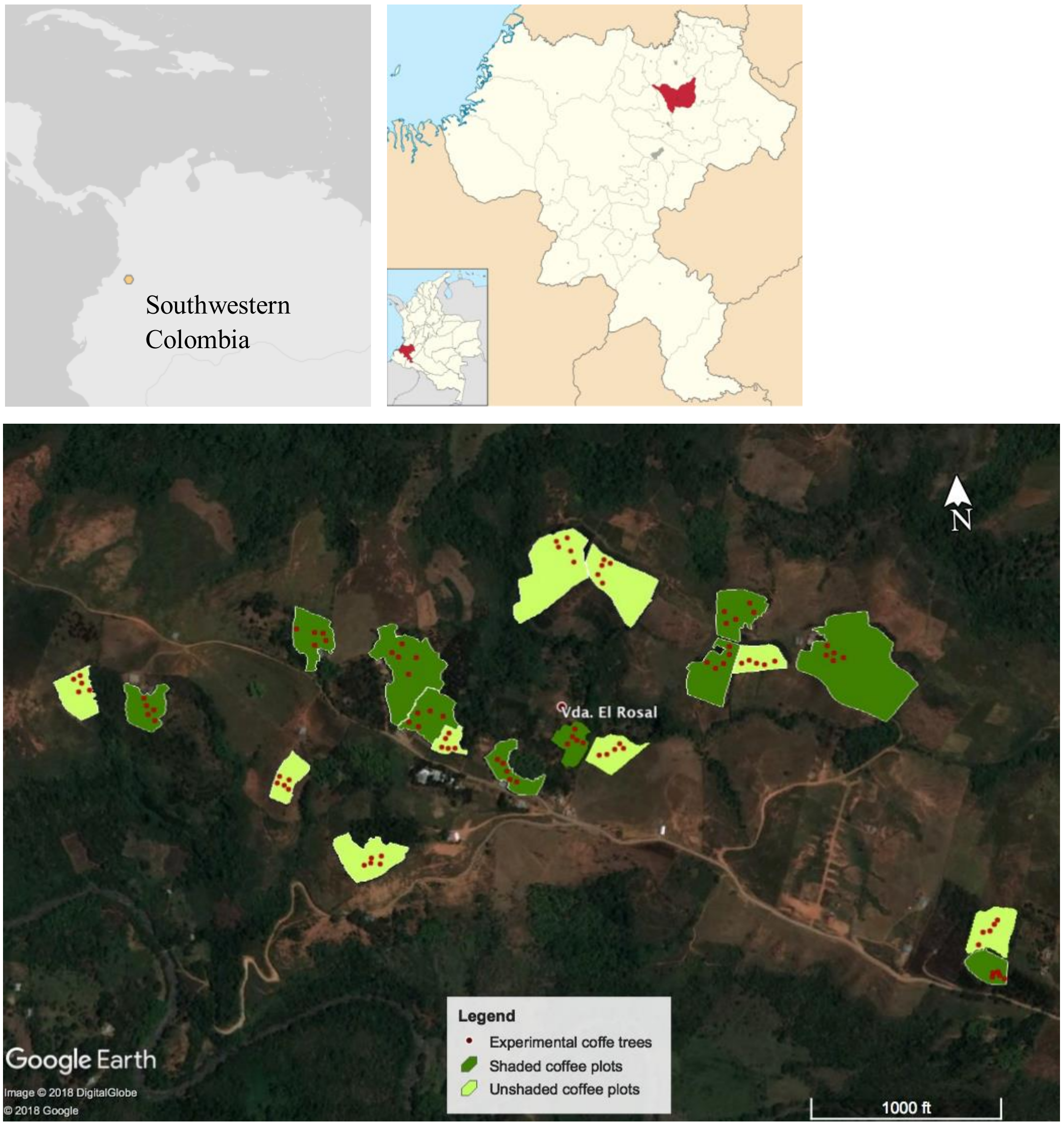

Figure A.1. Location of the study site showing the 20 plots (10 shaded coffee and 10 unshaded coffee plots) where coffee foraging ants were excluded and CBB infestation rates estimated. The 20 plots were distributed along El Rosal village, in Caldono Cauca (Southwestern Colombian coffee region).

A.2. R script for data analysis

Packages

```
require(lme4)
require(multcomp)
require(effects)
require(MuMIn)
require(ggplot2)

dat1 = read.csv("data_file.csv", head=T, sep=";")
head(dat1)
str(dat1)
```

Correlation test for all the nine variables (local + landscape-scale)

```
Variable = with(dat1,
as.data.frame(cbind(ant_presence,no_berries_ground,no_twigs_ground,leaf_litter_dept,
leaf_litter_volume,tree_cover,percent_coffee_perimeter,percent_other_crops_perimeter,
percent_non_cropped_perimeter)))

res=cor(Variable)
max(abs(res[upper.tri(res)]))
res

dat1$TOTAL.FRUITS.IN.THE.BRANCH =
as.numeric(as.character(dat1$TOTAL.FRUITS.IN.THE.BRANCH))
dat1$harvested_fruits = as.numeric(as.character(dat1$harvested_fruits))
dat1$prop_infested = as.numeric(as.character(dat1$prop_infested))
```

Specific objective #1. Model to evaluate how CBB infestation rates are affected by ants (figure 1)

```
dat0 = droplevels(dat1[complete.cases(dat1$prop_infested),])
mod1 = lmer(prop_infested ~ ant_presence  + (1|PLOT/COFFEE.TREE/PAIR), data=dat1)
```

Specific objective #2. Model to test the effect of ants and local factors over CBB infestation rates (table 1)

```
mod2 = lmer(prop_infested ~ ant_presence + no_berries_ground + no_twigs_ground +
leaf_litter_depth + leaf_litter_volume + tree_cover + (1|PLOT/COFFEE.TREE/PAIR),
data=dat1)
```

Specific objectives #3. Model to test the effect of local and landscape factors over CBB infestation rates (table 2)

A subset of the dataset containing the data where ants were present, were created as:

```
sub1 = subset(dat1, dat1$ant_presence == "A")
```

Model to test the effects of local and landscape variables on CBB infestation rates

```
mod_env = lmer(prop_infested ~
            (no_berries_ground)
          + (no_twigs_ground)
          + (leaf_litter_depth)
          + (leaf_litter_volume)
          + (tree_cover)
          + (plot_area)
          + (coffee_perimeter)
          + (other_crops_perimeter)
          + (non_cropped_perimeter)
          + (1|PLOT/COFFEE.TREE/PAIR), data=sub1)
```

Specific objective #4. Estimation of the AIC values for the separate and combined effects of significant local and landscape variables predicting CBB infestation rates (table 3)

```
mod_inter = lmer(prop_infested ~
                  no_twigs_ground
                * tree_cover
                * (other_crops_peperimeter)
                + (1|PLOT/COFFEE.TREE/PAIR), data=sub1)
```

CHAPTER 5

Synthesis

Even though the general objective of this dissertation was to generate quantitative information about biocontrols and CBB dynamics in coffee agroecosystems, this work also looked to provide management recommendations that may allow reducing the negative impacts of the most economically important coffee pest. This is why, the conclusions presented next include, when available and necessary, management suggestions based on the main results of each chapter. All the fieldwork from this dissertation was performed in Caldono-Cajibío region, one of the most important coffee areas in Colombia, and conclusions are mainly referred to this biogeographical zone if not mentioned otherwise.

In synthesis, this dissertation found from a comprehensive, systematized and replicable literature review performed to understand CBB enemies efficacy (chapter 1) that half of the studies analyzed where successful to control this borer. This pattern was true for different target organisms, including fungal entomopathogens, ants, parasitic wasps, birds, and nematodes. Of these taxa, ants were the group with the largest number of investigations that met the criteria to be categorized as successful CBB control.

However, only one study (focused on birds) analyzed the importance of landscape-scale variables and their effect on the successful control of this pest. Other reviews in this regard (Morris et al., 2018) have found similar results discussing mainly the lack of studies incorporating landscape-scale variables to measure ants effectiveness to control CBB. Likewise, relatively few studies (of the ones analyzed in chapter 1) evaluated the effect of different management practices (i.e., shade presence and organic / non-organic management) over control effectiveness of this pest. Among the studies that did measure these practices, almost half showed that there could be an effective control of CBB in organic-shaded coffee plantations (references from the review). Likewise, it can be highlighted that of all the studies evaluated and that counted as CBB successful biocontrols, where from only two coffee producing countries. In summary, these results allow us to conclude that more studies are needed that explicitly include 1) a greater number of taxa (individually or interacting), and 2) more relevant factors that at the local and landscape scales, help to evaluate in a more comprehensive way the mechanisms enhancing effective CBB biocontrol. These studies should be replicated as far as possible, throughout the different coffee producing regions worldwide in order to identify particularities, if any, concerning each studied landscape (Avelino et al., 2012).

After understanding the lack of knowledge regarding how local and landscape factors affects CBB biocontrols, chapter 2 sought to evaluate how such variables affect ants diversity. Ants were chosen as a focal group because of the well-reported importance to potentially control CBB (see Chapter I, ref). As for birds (Karp et al., 2013), our results on spatial patterns of ant diversity highlights the importance to maintain forest fragments and/or strips (or maybe even trees covering the coffee canopy) between coffee plantations, in order to maintain a high ant diversity within landscapes that incorporate coffee plantations.

Knowledge gathered in chapters 1 and 2 were the main motivation to set an experiment and posterior mathematical modeling approach (chapter 3), which aimed to implicitly evaluate how ants, and the interactions of local and landscape factors, explain CBB infestation rates. The mentioned approach helped to conclude that ants are indeed an important CBB biocontrol agent, but also that interactions of important local and landscape factors affect CBB infestation rates (similar results found elsewhere includes De la Mora et al. 2015 and highlighted by Morris and colleagues 2018).

All together these last mentioned results (from chapter 3) with conclusions from chapter 1 and 2, allowed to summarize that i) ant presence and diversity, and ii) the interaction of local (i.e., number of twigs in the ground, tree presence) and landscape factors (i.e., non-cropped area surrounding the coffee plantations) should be considered and explicitly managed in areas where coffee is the dominant crop. Other investigations have shown separately, similar results for other biocontrols (Johnson et al., 2010; Karp et al., 2013; Kellermann et al., 2008) suggesting that integral and simultaneous management of coffee agroecosystems should be incorporated as a common practice to reduce its significant pests (Stenberg, 2017). In practice, these management actions should not be that difficult to implement in a real-world scenario, and ideally, coffee farm owners might take part in this process (Aristizábal et al., 2012). Including owners can reduce expenses related to fieldwork and on the other hand, increase the probabilities for a new methodology to be adopted after benefits are visible and generalized among local producers (Jeanneret et al., 2016)

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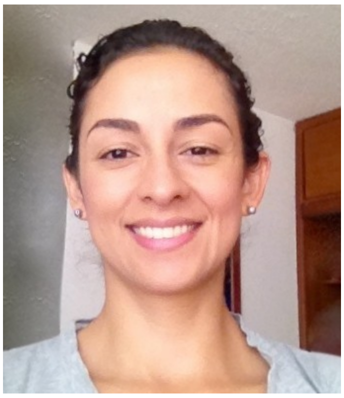
CURRICULUM VITAE

Selene Escobar Ramírez |



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-
Research interest

- Plant-insect interactions in tropical agroecosystems
- Ecosystem services and dis-services by ants (seed dispersal, natural pest control, herbivory, trophobiosis).
- Recovering of ecological functionality in agroecosystem through management of biodiversity.

PhD research topic

-
- My current work is related with natural control of coffee berry borer bug (Hypothenemus hampei) by generalist ants, and its effects on infestation rates and yield. Assessment of the effects of crop management practices at local and landscape-scale on natural pest control by ants in Colombian coffee crops.

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-
Master in Sciences–Biology (MSc) Department of Biology, Faculty of Science
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-
Published research papers

2016 Jiménez, E., García-Cárdenas, R., Escobar-Ramírez, S., Armbrecht, I. y Montoya, J. 2016. Ants in coffee plantations with different management intensity in Cauca, Colombia. 3154 registrers, published 26/10/2016. On line, http://ipt.biodiversidad.co/valle/resource.do?r=hormigas-cafetales-cauca

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-

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STATUTORY DECLARATION

„Herewith I declare that I have autonomously prepared the at hand thesis and used no other than the stated resources.“

Date: 02. 08. 2018 Signature: ______________________