DISSERTAÇAO

Instituto de Biociências

Universidade de São Paulo

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Efeitos da estrutura da paisagem no controle de pragas por formigas em cafezais

Landscape structure effects on ant-mediated pest control in coffee farms

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Cover Page

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Landscape structure effects on ant-mediated pest control in coffee farms

Dissertation presented to the Bioscience Institute of the University of São Paulo, to obtain a Master of Science in Ecology.

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Comissão Julgadora

Prof. Dr.

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Dedication

To my wonderful, hard-working, and beloved parents.

Epigraph

“For instance, on the planet Earth, man had always assumed that he was more intelligent than dolphins because he had achieved so much—the wheel, New York, wars and so on—whilst all the dolphins had ever done was muck about in the water having a good time. But conversely, the dolphins had always believed that they were far more intelligent than man—for precisely the same reasons.”

Douglas Adams, The Hitchhiker's Guide to the Galaxy

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Summary

General Introduction

Land change and ecosystem services

Humans have altered more than 75% of the Earth's ice-free land (Verburg et al. 2013), including at least 43% of natural habitats transformed into agricultural landscapes (Foley *et al.* 2011). With increasing agricultural expansion and land conversion, habitat fragmentation has intensified (Matson *et al.* 1997). Fragmentation causes disruptive impacts on ecological processes such as a decrease in landscape connectivity (Gonzalez *et al.* 2009), affecting the movement of organisms among habitats and their ecological functions (Mitchell *et al.* 2015). Another type of responsive ecological process that results from human landscape modification is an increase in the boundaries between agricultural and natural systems, facilitating a spillover edge effect movement of organisms from source populations to adjacent areas (Rand *et al.* 2006).

Habitat fragmentation and agricultural expansion are considered the main causes of biodiversity loss (Philpott *et al.* 2008). A review study across 35 years of projects monitoring fragmentation effects on several biomes and scales, show species richness decreases by 13 to 75% as landscape fragmentation increases (Haddad *et al.* 2015). A specific example from a study in the Brazilian Atlantic Forest indicates community integrity of amphibians, birds and mammals decreases as fragmentation increases (Banks-Leite *et al.* 2015). Precisely, the community integrity of vertebrates is maintained merely until 30% of the landscape remains natural habitat (Banks-Leite *et al.* 2015). However, a clear understanding of how reduction of species diversity might affect ecological processes across landscapes is yet to be completed. Fulfilling this gap is of extreme importance in complex landscapes as that is mostly what is left on Earth, a composition of mosaics of native habitat fragments and agricultural areas (Rand *et al.* 2006).

Land conversion and agricultural intensification not only alter landscape structure, ecological processes, and species diversity, but also the ecosystem services these organisms provide (Cardinale *et al.* 2012). Ecosystem services are considered the benefits humans obtain from nature directly or indirectly (Daily 1997). Two of the ecologically and economically most influential ecosystem services are pollination and pest control. Pest control is the regulation of pests and diseases in natural or agricultural systems through processes such as predation, parasitism or competition (Pittman and McCormick 2010). Pest control and pollination are examples of ecosystem services driven by mobile organisms vulnerable to landscape fragmentation (Mitchell *et al.* 2015). It was estimated that the economic value of pest control services in the world, is a total of US $417 dollars per hectare per year (Costanza *et al.* 1997). In Brazil alone, it was calculated that pests cause a 7.7% production loss per year, or approximately US$17.7 billion dollars (Oliveira *et al.* 2014).

The relationship between biodiversity and ecosystem services is not completely understood (Cardinale *et al.* 2012). However, there is evidence that ecosystem services are more threatened in tropical regions because land cover loss is occurring more rapidly due to intensive agricultural, industrial, and human population pressures (Achard *et al.* 2014). One of the natural habitats that has been altered the most, mainly as consequence of agricultural expansion, is the Brazilian Atlantic Forest, where only 12% to 16% of the original forest remains (Ribeiro *et al.* 2009) (Figure I 1). The Atlantic Forest is not only considered a biodiversity hotspot (Myers *et al.* 2000), but also provides a wealth of ecosystem services regionally and globally (Ferraz *et al.* 2014; Joly *et al.* 2014).

Despite some punctual experiments and very general extrapolations at larger scales, we still lack an in-depth knowledge of the mechanisms that regulate ecosystem services. Thus, it is essential to study the impacts of land-use change and agricultural intensification in these highly modified and fragmented landscapes, and how those impacts affect ecosystem services. Ideally, we will soon be able to design multifunctional landscapes capable of maintaining biodiversity and ecosystem services while sustaining agricultural productivity. To reach this goal, we need to better understand the relationships among landscape structure patterns, biodiversity, ecological processes and ecosystem services.

Study system: ants and CBB control in coffee farms

Coffee is one of the most valuable commodity products in the world, second only to petroleum (Perfecto & Vandermeer 2002). Coffee is cultivated globally, but it grows best and is most explored in tropical biodiverse developing countries (Ricketts *et al.* 2004). It is estimated that the complete production process employs more than 100 million people around the world (Bunn *et al.* 2015; Fair Trade Foundation 2012). Its social, economic and cultural significance is unquestionable. Around the globe, there are several management types, from organic practices to intensive use of chemical insecticides and fertilizers. There is as well an array of styles to produce coffee, from traditional sun coffee plantations to shaded agroforestry systems, or "rustic coffee" systems, embedded below native forest canopy (Perfecto & Vandermeer 2002; Donald 2004). All these coffee systems result in agricultural matrices with different qualities for native habitat species (Vandermeer & Perfecto 2007). Therefore, there is a gradient of landscape complexity and agricultural intensification in coffee-dominated landscapes, which thus serves as natural, experimental platforms to study the consequences of transforming natural vegetation into agricultural lands (Perfecto, Vandermeer & Philpott 2014).

The Brazilian Agricultural Research Corporation estimated that at least 2.21 million hectares of Brazil's natural habitats have been converted to coffee crops (Embrapa 2016) (Figure I 1). Brazil is the main producer and exporter of coffee in the world, producing 35% of the world's commercialized coffee (USDA 2015). However, most of these coffee crops (90%) are produced as direct sun plantations (Ricci, Araújo & Franch 2002). For these reasons it is important to study the ecological interactions, which could be either beneficial or detrimental, involved in the transformation of this extensive use of land for coffee crops with the remaining and endangered natural forest systems.

Coffee crops suffer impacts by several pests, affecting negatively coffee yield and increasing the use of chemical insecticides. The worst, most economically influential coffee pest in the world is the coffee borer beetle (CBB), *Hypothenemus hampei*, Ferrari (Coleoptera: Curculionidae) (Vega 2009). These small beetles (1-2 mm) are coffee berries specialists. CBB females drill through coffee berries to lay eggs, which then feed off the coffee beans (there are two beans per coffee berry). Consequently, CBB reduces coffee's quality, weight and therefore, its price causing Brazilian coffee farmers to lose between $215-358 million dollars per year (Oliveira et al 2013).

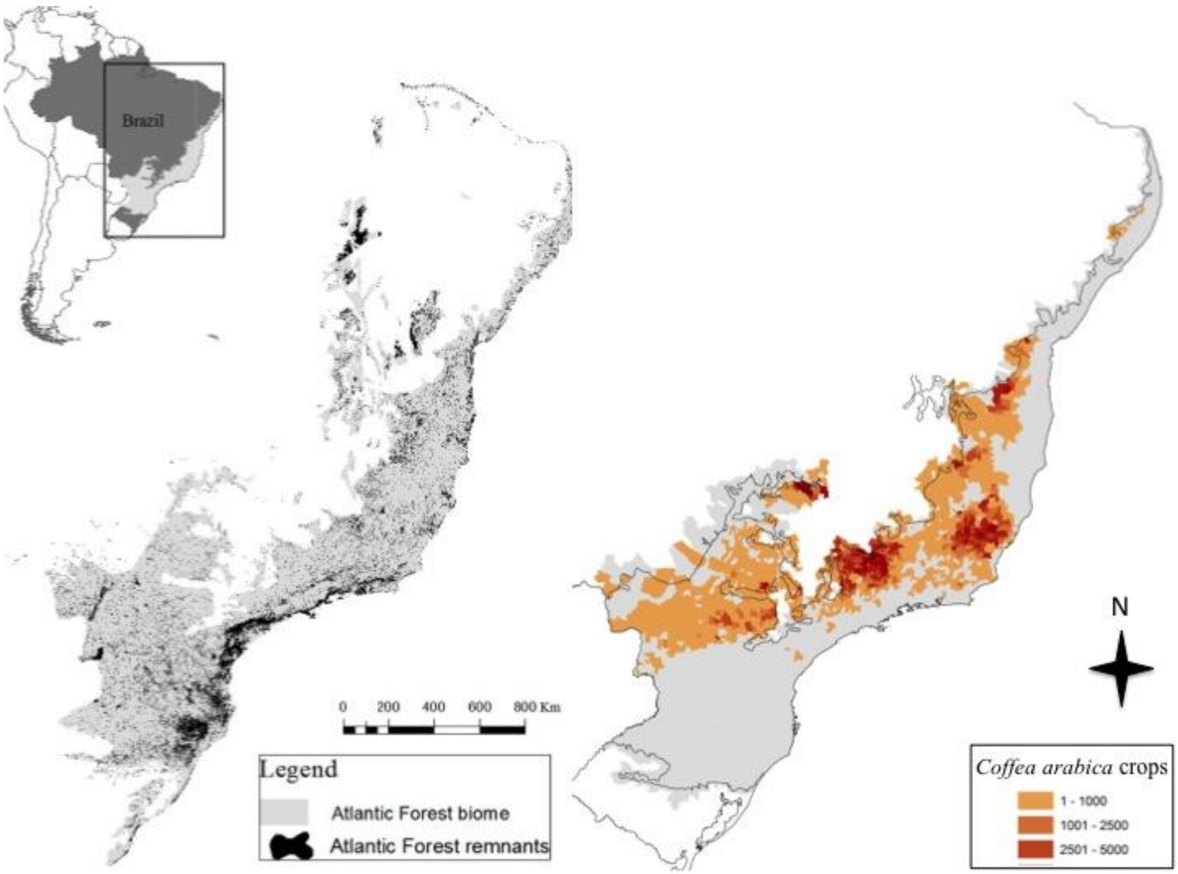

Figure I 1. Original distribution of the Atlantic Forest biome, current forest remnants, and extension and intensity of *Coffea arabica* croplands.

Being such an economically influential commodity, and being responsible for such drastic landscape transformations, there has been quite some focus on studying the relationships among forest loss, biodiversity and ecosystem services in coffee agroecosystems. We know from studies in traditionally grown shaded coffee agroecosystems in Central America, Colombia and a few in the Caribbean and Africa that ants predate and control CBB (Philpott & Armbrecht 2006; Avelino *et al.* 2012). Also, there are indications that CBB control services are regulated by the surrounding landscape structure (Armbrecht & Gallego 2007; Gonthier *et al.* 2013). However, there have been few studies in Brazilian coffee agroecosystems of sun coffee plantations adjacent to a highly fragmented Atlantic Forest. Rather, in Brazil little is known about pest control services by ants. Ants in agriculture are usually grouped and generally perceived as pests themselves, principally accredited to leaf-cutter ants (Philpott & Armbrecht 2006). There are, however, few evidence from Dias *et al.* (2012) that show a significant reduction of ant species diversity, relative to the surrounding native Atlantic Forest fragments. Which suggests that CBB control can also be affected by forest loss. Nonetheless, more studies are needed in order to better understand the influence of landscape structure on the composition of ant communities and on the ecosystem services they provide in highly fragmented landscapes.

Being able to test whether and how this pest control service is modulated by its surroundings are unique opportunities and exciting challenges. It could change the perception of farmers towards ants and contribute to better designed agricultural landscapes. It could be a positive economical reinforcement for coffee producers by decreasing use of insecticides and by reducing the loss due to CBB attacks. Additionally, learning more about ecosystem services provided by ants in coffee-dominated landscapes can contribute to protect forest remnants, the biodiversity that inhabits them, and simultaneously increase coffee yield. Resulting, presumably, in a win-win situation (Howe *et al.* 2014). More specifically, it is fundamental to study the ecological implications of forest loss and land-use change on ecosystem services supply (natural habitats), flow (movement or organisms, people and matter), and demand (level of service provision) (Mitchel *et al.* 2015). It could be one of the means to promote conservation policies that are beneficial and well perceived among producers, policy makers and conservationists.

Objectives and hypotheses

We know ants contribute with pest control of CBB in shaded coffee plantations (Bustillo *et al.* 2002) and that landscape structure can influence ecosystem services (Folgarait, 1998; Tscharntke *et al.* 2008). Therefore, our main objective with this Master's dissertation was to test the ability and intensity of pest control provided by ants in highly fragmented landscapes and in sun coffee production. Specifically, we want to better understand the ecological processes that relate landscape structure with pest control.

In order to explore this topic, we first studied how landscape structure affected ant-mediated pest control services in sun coffee systems. We tested whether CBB pest control is influenced by distance to the nearest forest fragment, forest cover (in a 2 km-level and 300 m-level), and coffee cover (in a 300 m-level). We measured CBB control with three indicators: CBB presence, CBB infestation per branch, and CBB damage per infested coffee bean. This is the main chapter of this dissertation, which is organized as a manuscript ready for submission in the *Journal of Applied Ecology*.

Additionally, during fieldwork for this dissertation we obtained data to explore two other complementary questions that will be analyzed after the dissertation's defense. The first is the relationship between forest cover and ant community composition in coffee agroecosystems. Specifically we will test whether forest cover (in a 2 km-level and 300 m-level) can modulate ant community composition, comparing inside forest fragments and the coffee matrix. This topic will be developed in collaboration with the undergraduate student Guilherme Prata Gonçalves from the Federal University of São Paulo. We are in the process of identifying the collected specimens of ants during fieldwork in order to proceed with data analyses.

The second question to be developed in a near future is whether there are synergies and trade-offs among CBB control providers in coffee farms (i.e. ants, birds and bats) and the influence of landscape structure in these processes. This issue is being developed in collaboration with two other Master's students, Emilien Rottier and Felipe Librán, from Angers University and University of São Paulo, respectively. We are specifically testing whether distance to the nearest fragment, forest cover (50 m – 2 km-levels), and coffee cover (50 m – 2 km-levels) influence CBB pest control by birds, bats, and ants. Data has been collected during a 12-month fieldwork and it is currently being analyzed.

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Capítulo Único

A estrutura da paisagem influencia o controle de pragas por formigas nos cafezais

Natalia Aristizábal and Jean P. Metzger

Resumo

1. Os serviços de controle de pragas têm papel fundamental para a sustentabilidade da agricultura, porém ainda pouco se sabe sobre como a estrutura da paisagem, tanto em termos de composição (tipos de uso e cobertura dos solos) quanto de configuração (proximidade a fragmentos florestais, grau de fragmentação, entre outros), regula a provisão destes serviços em paisagens fragmentadas.
2. Nesse estudo, testamos a capacidade de formigas promoverem o controle da broca-do-café (CBB), a principal praga do café em termos econômicos, e testamos ainda se a provisão desse serviço varia em função da estrutura da paisagem. Medimos o controle de CBB em plantações de café a pleno sol em dez paisagens do Sudeste do Brasil, que representavam um gradiente de cobertura florestal e de café. Utilizamos experimentos de exclusão de formigas, dispostos a diferentes distâncias dos fragmentos florestais, e comparamos o nível de controle de pragas nos experimentos e fora deles. Testamos como o controle de CBB é afetado pelas interações da exclusão de formigas com parâmetros da estrutura da paisagem, incluindo a proximidade a fragmentos florestais, a cobertura florestal (em raios de 2 km e 300 m) e a cobertura de café (em raios de 300 m). Consideramos três indicadores de controle de pragas: presença de CBB, grau de infestação por CBB e o dano aos grãos de café por CBB.
3. As formigas diminuem fortemente a presença de CBB e o dano aos grãos de café por CBB. Além disso, o controle de CBB ocorre, independentemente da sua proximidade aos fragmentos florestais, mas aumenta após 25 m, sugerindo que as formigas que prestam esse serviço estão adaptadas às condições ambientais das plantações de café a pleno sol.
4. A existência de pelo menos 35% de cobertura florestal, num entorno de 2 km, reduz a infestação de CBB e o dano aos grãos de café. A expansão da cobertura de café aumenta a presença de CBB, mas diminui o dano aos grãos de café.
5. *Síntese e aplicações.* Esse estudo apresenta novas evidências que as formigas provêm controle de CBB e esse serviço é modulado pela estrutura da paisagem. Este estudo fornece assim dados importantes para planejar paisagens de cultivo de café que ao mesmo tempo permitam maior controle de CBB e conservação de habitats naturais.

Palavras chaves: *Broca do Café, Coffea arabica, Formicidae, Mata Atlântica, Serviços ecossistêmicos, planejamento de paisagens*

Single Chapter

Landscape structure influences ant-mediated pest control in coffee farms

Natalia Aristizábal and Jean P. Metzger

Abstract

1. Pest control services play a fundamental role in agriculture sustainability. However, little is known on how they are regulated by landscape composition (i.e. land-use and land cover change) and configuration (i.e. proximity to forest fragments and fragmentation intensity).
2. We measured whether landscape structure influences the ability of ants to control coffee berry borer (CBB), coffee's most economically influential pest, in sun coffee agroecosystems in Southeastern Brazil. We measured pest control among 10 landscapes that represented a gradual difference in forest and coffee cover. We manipulated ants through exclusion experiments (set at varied distances from forest fragments) and compared pest control inside and outside exclusion experiments. We tested whether CBB control is influenced by interactions of ant exclusions with landscape structure metrics, including distance to forest fragments, forest cover (2 km and 300 m-levels), and coffee cover (300 m-level). We considered three indicators of pest control: CBB presence, CBB infestation, and CBB bean damage.
3. Ants provide CBB control, strongly reducing CBB presence and bean damage. Also, CBB control is maintained regardless from its proximity to forest fragments, but increases after 25 m (hinting ants who provide this pest control service are adapted to habitat conditions in sun coffee farms).
4. Existence of at least 35% of forest cover in radii of 2 km reduces CBB infestation and bean damage. Results suggest further that expanding coffee cover increases CBB presence, but decreases bean damage.
5. *Synthesis and application*. This study presents new evidence of ants as efficient providers of CBB control in sun coffee agroecosystems and how this service is influenced by landscape structure. This study provides important data useful to adequately plan coffee landscapes with both enhanced CBB control as well as potential for conservation of natural habitats.

Keywords: *Atlantic Forest, Coffea arabica, Coffee Berry Borer, Ecosystem services, Formicidae, Landscape design*

Introduction

Tropical coffee agroecosystems are known to benefit from several ecosystem services (Classen *et al.* 2014; Perfecto, Vandermeer & Philpott 2014). One of these services is the regulation of the principal coffee pest in the world, known as the 'coffee berry borer' (CBB), *Hypothenemus hampei* (Vega *et al*. 2009). This beetle drills through coffee berries to lay eggs, which then feed off the coffee bean, reducing coffee's quality, weight and yield (Vega *et al.* 2009). In Brazil alone, the principal coffee producer in the world, the losses by CBB activity represents a $215–358 million dollar loss per year (Oliveira *et al.* 2013). Considering that more than 100 million people depend on coffee production (Bunn *et al*. 2015; Fair Trade Foundation 2012) and that over 10 million hectares have already been transformed for coffee production worldwide (FAO 2016), the search for sustainable ways to naturally control CBB in coffee agroecosystems is eminent for economical and conservation reasons (Jaramillo, Borgemeister & Baker 2006).

Among all species known as natural enemies of CBB, ants stand out because they are usually resistant to habitat disturbance and therefore exceptionally abundant in tropical systems (Hölldobler & Wilson 1990; Fernández 2003). Several generalist ant species have shown prey removal adeptness in field studies and observations (Bustillo, Cárdenas & Posada 2002; Philpott & Armbrecht 2006; Avelino *et al.* 2012). Additionally, experiments with lab colonies show ants' efficiency to remove and carry CBB to their nests (Larsen & Philpott 2010). Moreover, exclusion experiments in coffee agroecosystems show several ant species reducing CBB colonization (Gonthier *et al.* 2013) and predating CBB (Armbrecht & Gallego 2007).

Pest control is directly or indirectly affected by changes in landscape composition and configuration (Tscharntke *et al.* 2008). Land transformations by humans alter landscape structure, which can thus affect the ecological processes that regulate pest control, acting on the persistence and movement of predators at the landscape level (Boesing, Nichols & Metzger 2016). An increase in agricultural-natural habitat edges can potentially lead to changes in pest and predator diversity and abundance (Rand, Tylianakis & Tscharntke 2006). For instance, increasing isolation from native habitats decreases abundance and activity of natural enemies (Bianchi, Booij & Tscharntke 2006; Karungi et al. 2014). Additionally, in coffee agroecosystems, a decline in habitat quality causes a loss in predator ant species richness (Perfecto & Vandermeer 2002), and a reduction in forest habitat and landscape heterogeneity can lead to a decrease in CBB control and CBB removal (Perfecto & Snelling, 1995; De la Mora, Murnen & Philpott 2013). Despite agricultural intensification can be related to simplification of agricultural landscapes (Bianchi, Booij & Tscharntke 2006), expansion of local coffee cover has sometimes been associated with an increase in CBB prey removal (De la Mora; García-Ballinas & Philpott 2015). All these complex patterns and processes involve not only landscape structure change, but also inter-specific interactions that are difficult to unravel. Therefore, it is needed a more comprehensive understanding of the effects of land use and land cover change on the ecological processes that regulate pest control in coffee agroecosystems.

Most of the studies aimed at unraveling CBB control services in coffee agroecosystems come from regions where coffee is primarily grown in shaded agroforests and polycultures (e.g. Gonthier *et al*. 2013, Larsen & Philpott 2010), but few have been conducted in areas where sun coffee dominates, such as Brazil. Therefore, it has yet to be tested whether CBB control service is provided in intensively managed sun coffee monoculture farms, and how this service is modulated in highly fragmented landscapes. Learning more about pest control services provided by ants in sun coffee landscapes could potentially contribute to protect forest remnants and the biodiversity that inhabits them. It could also improve coffee yields and benefit farmers, enabling thus appropriate steps toward the reconciliation between coffee production and conservation (Vandermeer & Perfecto 2007).

Because landscape structure can influence ecosystem services (Folgarait 1998; Tscharntke *et al.* 2008; Mitchell *et al.* 2015), the fundamental goal of this study was to examine ant-mediated pest control services in coffee farms among landscapes with different compositions and configurations. Specifically, we tested whether distance to the nearest forest fragment, forest cover, and coffee cover modulate pest control of CBB by ants. We did this by experimentally excluding ants from coffee branches during a year of coffee production in southeastern Brazil. We measured pest control with three indicators in order to consider different ecological processes in which ants are possibly providing CBB control: 1) *CBB presence or absence* per branch was used to test the ability of ants to prevent CBB from colonizing coffee berries; 2) *CBB infestation* was used to test the capacity of ants to impede CBB infestation over a branch once at least one coffee berry had been colonized; and 3) *CBB bean damage* was used to test the ability of ants to predate CBB inside infested coffee berries and restrain further bean damage. We expect that *CBB presence, CBB infestation*, and *CBB bean damage* would be higher in exclusion of ants. Furthermore, we predict that *CBB presence*, *CBB infestation*, and *CBB bean damage* control will have an inverse relationship with forest cover, and a direct relationship with distance to nearest forest fragment and coffee cover around exclusion experiments.

Methods

Study area

This study was developed in one of the most traditional areas for coffee production in Brazil, in the limit between the states of Minas Gerais and São Paulo. Brazil produces 35% of the commercialized coffee in the world (USDA 2015), and the states of Minas Gerais and São Paulo produce nearly two thirds of that coffee (Embrapa 2016). Nearly 90% of the coffee in Brazil is produced as non-shaded sun coffee (Ricci, Araújo & Franch 2002) in an area expanding across more than 2 millions hectares (Embrapa 2016). Land in the study region is primarily used for agricultural activities within a matrix that contains remnants of native Atlantic Forest, an endangered forest with only 12% to 16% of its original forest remaining (Ribeiro *et al.* 2009). The Atlantic Forest is considered a biodiversity hotspot (Myers *et al.* 2000), and also an important supplier of ecosystem services regionally and globally (Ferraz *et al.* 2014; Joly *et al.* 2014).

We selected 10 landscapes, considered as circular sample areas of 3 km radii, that capture a range of forest cover (9% to 34%) within coffee farms (Figure 1). Landscapes were composed of heterogeneous mosaics of coffee, forest, pasture, sugar cane, water, human settlement, young regenerating forest, and eucalyptus plantations (Figure S 1, Table S 1). In each landscape we fixed three sites with ant exclusion experiments (see description below), except for one landscape that could only have two sites for logistical restrictions (one of the farms was abandoned and sold). Therefore, we had a total of 29 experimental sites involving 17 different farms. Experimental sites in the same landscape were placed at least 100 m apart from each other. To avoid bias, coffee farms included in the study applied similar management procedures, including common use of fertilizers and pesticides (which was recorded from interviews with farmers from 2013 to 2015), and manual harvest (except for one property - which included three experimental sites - that harvests mechanically).

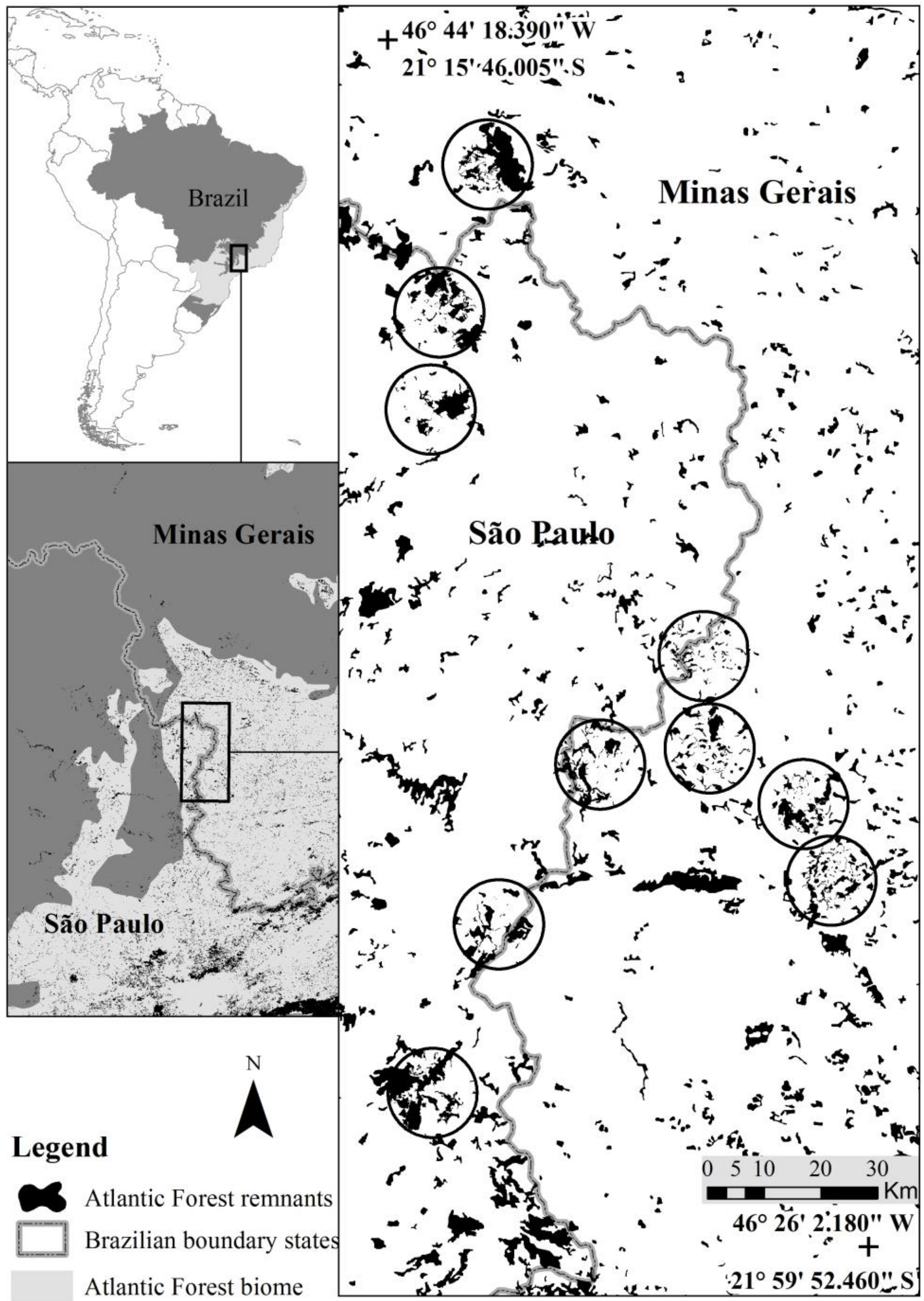

Figure 1. Study region and geographical location of the 10 landscapes (3 km radius) in the Brazilian states of Minas Gerais and São Paulo.

Landscape metrics, explanatory variables, and site selection

We used high-resolution satellite images from ArcGIS 10.3 basemap imagery (2009 to 2011) with a reference scale of 1:5.000 and 1 m resolutions to map the landscapes, and classify and quantify land uses (Figure S 1, Table S 1). Landscape composition and configuration were analyzed at two different levels: a 2 km-level radius for each selected landscape and a 300 m-level radius around each experimental site (see below). We chose the 2 km radius to represent a broad landscape level (which still had a 1 km buffer of mapped area around it), and a 300 m radius level based on ant foraging distances (Traniello 1989).

Using FRAGSTATS 4.2, we measured the following landscape metrics as explanatory variables: distance to the nearest forest fragment, forest cover at the 2 km-level, and forest cover and coffee cover at the 300 m-level. All pixels inside each landscape were analyzed in radii of 300 m to better understand the relationship between distance to the nearest forest fragment and amount of native forest cover around coffee crops in this region (Figure 2). To include the broadest range of existent forest cover in a radius of 300 m (0–85 %), we selected experimental sites at a maximum distance of 100 m from forest fragments (Figure 2).

Exclusion experiments were selected initially to test local effects of proximity to the nearest forest fragment and amount of forest in radii of 2 km and 300 m. However, after the first field seasons we recognized how much ants were using the coffee matrix to nest and we decided to add the amount of coffee cover in radii of 300 m as an explanatory variable in our study. Therefore, our study design finally included all possible combinations among our landscape variables of landscape forest cover (10–55% at 2 km-level), local forest cover (0–85% at 300 m-level), distance from a forest fragment (0–100 m), and local coffee cover (5–80% at 300 m-level).

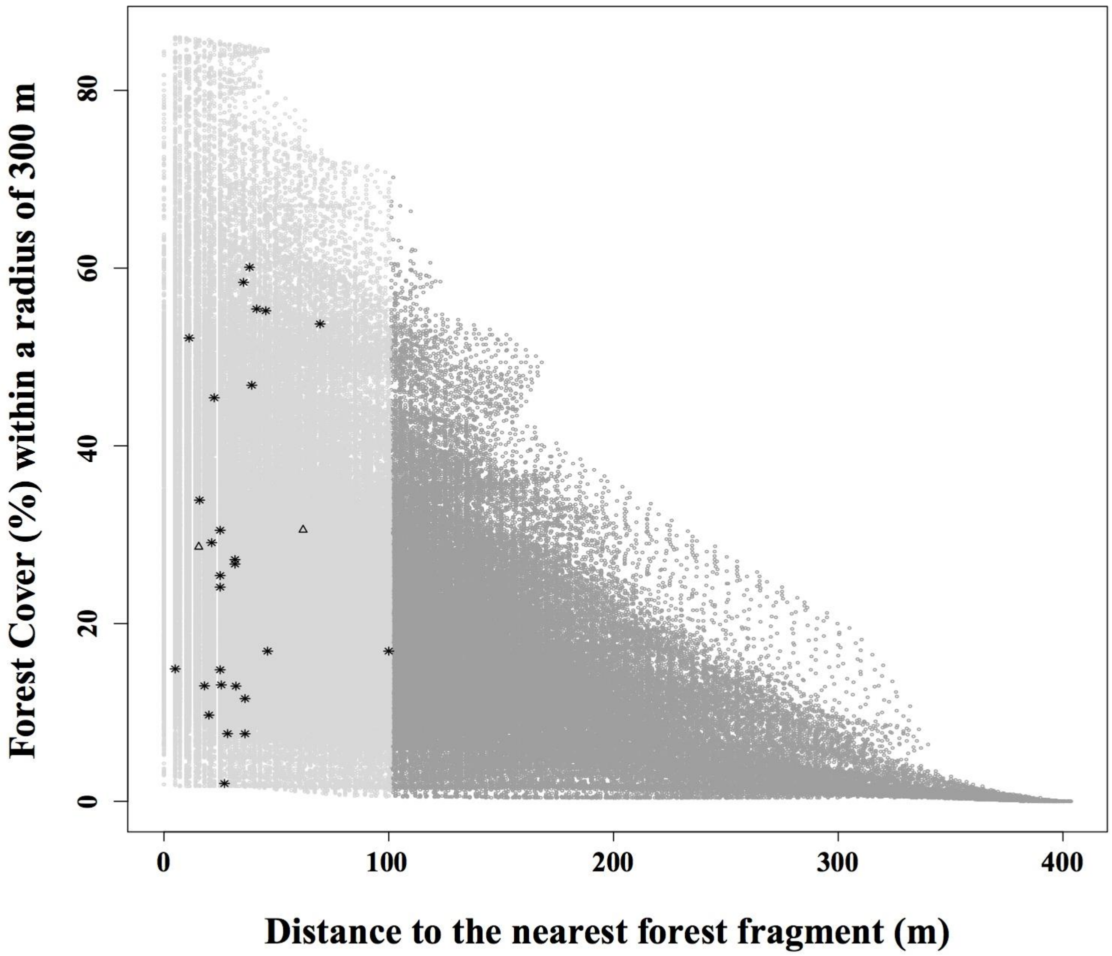

Figure 2. Relationship between forest cover (%) within a radius of 300 m and distance to the nearest forest fragment. Each point denotes a coffee pixel from the satellite images of our 10 landscapes. In light gray, pixels below 100 m distances from which we selected our experimental sites (black asterisks = 27 included, triangles = 2 not included in the analyses). In dark gray, pixels from our landscapes not considered for the selection of our experimental sites.

Ant exclusion experiments

To test the role of ants in CBB control, we experimentally manipulated presence of ants in selected branches of coffee plants during the 2014–2015 production season. We placed 10 exclusion experiment replicates per experimental site (a total of 290 coffee plants), right after the main flowering period of October 2014. This allowed us to ensure that coffee berries were initially CBB free. We only used *Coffea arabaica* plants in its varieties Catuaí and Catucaí, which are physiologically similar because Catucaí is a cross from Catuaí and another variety

(Icatú). In each coffee plant, we selected two similar branches with the same height and same number of flowers. We then randomly selected one of the two branches as the treatment branch to implement ant exclusion experiments and the other as its control. We excluded ants by first isolating the branches by tying away any other branch that would or could potentially come into contact. Next, we put Tree Tanglefoot Insect Barrier along 10 cm of the branch, after the first seven nodes, from the tip to the base (Figure S 2). This physical barrier excluded any terrestrial invertebrates, including ants. We visited each experimental site once a month to maintain and retouch exclusion experiments until June 2015. We also used these monthly visits to count on each control and exclusion branch (a total of 580 branches), the number of ants seen during five minutes of active observations, number of coffee berries, and number of coffee berries with CBB. We marked but did not manipulate control branches, except for a small smidge of Tanglefoot that would not exclude ants but would control for any effect of the smell or color of Tanglefoot on the CBB.

Pest control indicators: CBB presence/absence, infestation, and bean damage

We considered three response variables or indicators of CBB control to test different ecological processes in which ants are possibly providing CBB control and landscape structure could be influencing them (see objectives). *CBB presence/absence* was considered when there was at least one indication of CBB on any of the coffee berries of the branch. Absence was considered when none of the coffee berries on the branch had CBB. CBB infested berries, or bored berries, show a hole of ~ 2 mm diameter that is left by an adult female as it enters to lay its eggs. The second indicator was *CBB infestation*, the percentage of coffee berries infested with CBB out of the total number of coffee berries produced per branch. Finally, *CBB bean damage* was the percentage of damage by CBB on bored coffee beans. On our last visit in June 2015, right before farmer's harvesting time, we collected all coffee berries in our experimental branches. We separated bored from non-bored berries and opened all bored berries to determine the damage to each of the two coffee beans inside each coffee berry. We did this by measuring with a metric ruler the size of the coffee bean and the distance travelled and damaged by the CBB in each as a proxy of the bean damage percentage.

Data analysis

Because we were interested in testing pest control of CBB, measuring CBB control was not possible when CBB was absent from an entire experimental site. Consequently, we removed two experimental sites from the dataset that did not show evidence of CBB presence in any of the control branches (hence, neither in the treatment branches). Thus, in total, we analyzed a subsample that included all 10 landscapes, but only 27 (out of 29) experimental sites. We tested the difference in CBB presence between ant exclusion and control branches with a paired chi-square "goodness of fit" test. We also performed a paired *t*-test to examine the difference in CBB infestation per branch. To compare CBB bean damage between exclusion and presence of ants, we implemented a non-paired *t*-test using as testing unit each bored berry, as opposed to the paired branches.

We tested for collinearity among the explanatory variables and none of them were significantly correlated (> 0.69). Therefore, all four explanatory variables were used all further analyses. For each of the three response variables (each pest control indicator), we performed backwards model selection by likelihood ratio-tests. We used generalized linear mixed models (GLMM) with the 'glmer' function with a binomial distribution and a logit-link function in the 'lme4' package (Bates *et al.* 2015) in R (R v 3.2.3 Development Core Team, 2015). All model selections started with a full model that included additive effects from the interaction of ant exclusion (presence or absence) and all landscape explanatory variables. For the CBB presence and CBB infestation variables we included as random effects landscape's IDs, experimental sites' IDs nested inside landscape's IDs, and plant's IDs nested inside experimental sites. This last random factor was to pair each treatment to its control per coffee plant. Otherwise, for the CBB bean damage variable we included as random effects only landscape's IDs and experimental sites' IDs nested inside landscape's IDs because our individual was each CBB infested berry, which was not always paired to its control. For the CBB infestation and CBB bean damage variables we used the 'cbind' function to calculate the percentages internally in the models.

Results

Provision of CBB control by ants

Out of the grand total of 20.308 coffee berries tracked during our field seasons, 2.078 coffee berries were infested with CBB (10%). Infested coffee berries were found in 47% of the total of branches followed across all 10 landscapes and 17 different properties. CBB was found in 51% of ant-excluded branches and in 43% of control branches. The presence of ants reduced 19% CBB presence more than expected by chance alone ($\chi^2 = 30.79$, df = 3, $p < 0.0001$, Table 1). Yet, there was not a significant difference in percentage of CBB infestation per branch between ant exclusion and control branches ($p = 0.2$). Nevertheless, out of the 2.078 bored berries opened and measured for CBB damage, the mean percentage of damage per coffee bean was 35% in the presence of ants and 71% in exclusion of ants ($p < 0.001$, Figure 3).

Table 1. CBB presence frequency in ant exclusion experiments. A significant association between the presence of ants and *CBB presence* was observed ($\chi^2 = 30.79$, df = 3, $p < 0.0001$).

	CBB present only in exclusion branches	CBB present in both branches	CBB present only in control branches	CBB absent from both branches	Total
Observed	57	80	36	96	269
Expected	67.25	67.25	67.25	67.25	269

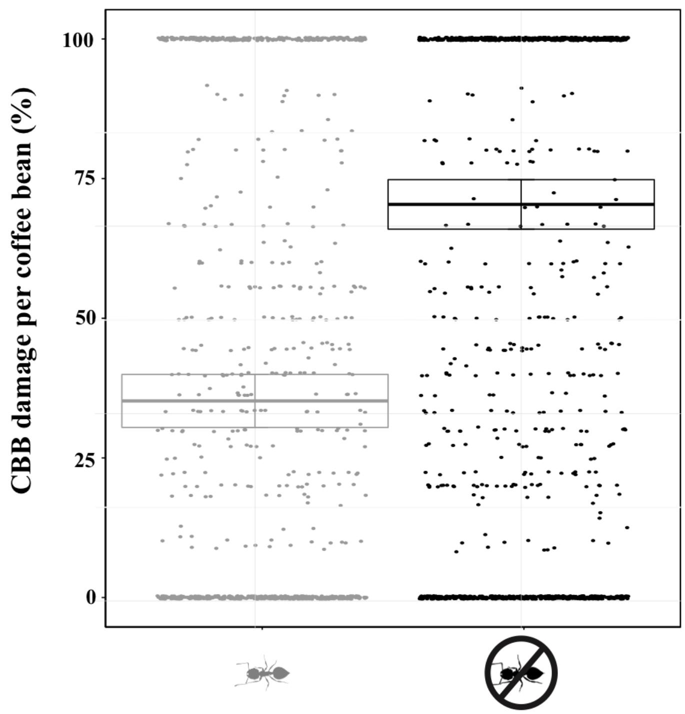

Figure 3. *CBB damage* percentage per infested coffee bean in exclusion and presence of ants ($p < 0.001$, n = 2.078). Boxes represent mean values ± standard errors.

Presence or absence of CBB per branch

Model selection analysis for the binary data indicating CBB presence or absence predicted a model that included a significant interaction between ant exclusion and coffee cover at the 300 m-level, and the additive effect of distance to the nearest forest fragment (Figure 4, Table 2, Table S 2). CBB presence increased slowly but steadily when ants were absent as the percentage of coffee cover increased at the 300 m-level ($p = 0.06$). However, in the presence of ants, CBB presence increased rapidly and non-linearly with higher coffee cover (Figure 4 A). Additionally, we found higher CBB presence as distance to the nearest forest fragment increased ($p = 0.09$), where at all distances from the fragment, CBB presence was always higher in the absence of ants (Figure 4 B). The adjusted deviance of this model explained 38% of the data variance. The residuals of the model plotted against its fitted values were well distributed and they adjusted to a normal distribution. Also, cook's distances of the model showed few points away from the adjusted, but these were not outliers influencing the analyses and were maintained.

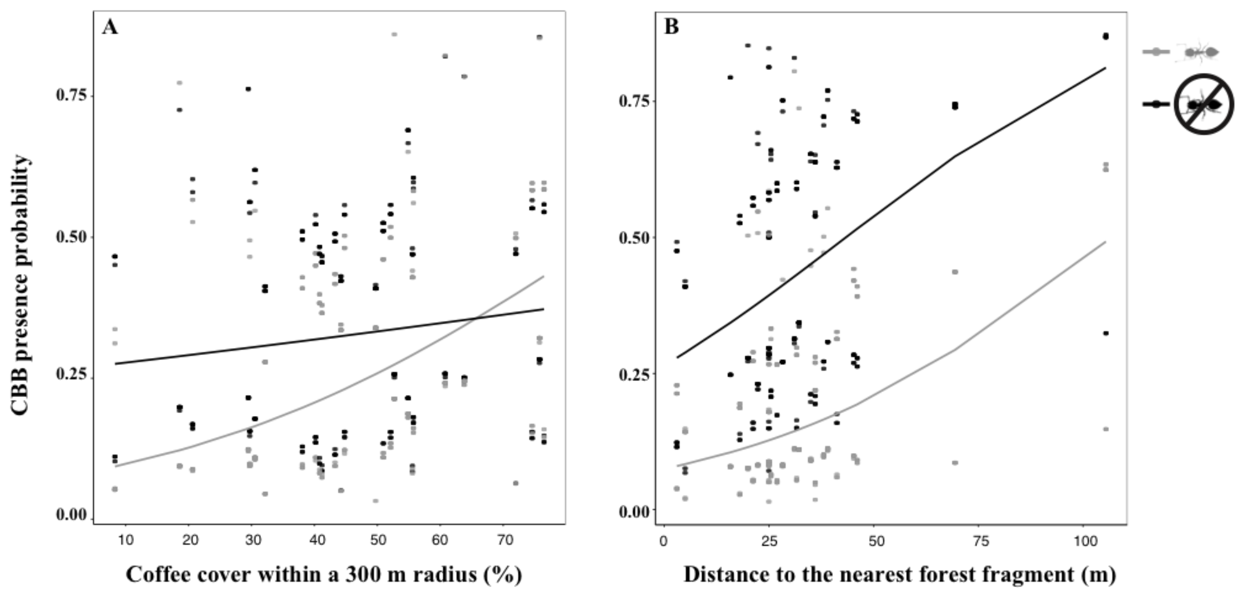

Figure 4. *CBB presence* probability per branch in response to an additive effect of a significant interaction between ant exclusion and coffee cover (300 m-level) (A) and distance to the nearest forest fragment (B).

Table 2. Model (GLMM) results for the fixed effects of ant exclusion and landscape variables on *CBB presence* per branch (n = 539, df = 8).

Fixed effects	Estimate	Std. error	2.5%	97.5%	*p*
Coffee (300 m)	0.51	0.29	-0.07	1.11	0.08
Control (presence of ants)	-0.39	0.28	-0.97	0.17	0.16
Treatment (ant exclusion)	0.04	0.28	-0.52	0.61	0.87
Distance to the nearest forest fragment	0.46	0.26	-0.08	1.01	0.09
Coffee (300 m) : Treatment (ant exclusion)	-0.40	0.21	-0.82	0.01	0.06

Percentage of CBB infestation per branch

For CBB infestation, the most informative model included an interaction between ant exclusion and distance to the nearest forest fragment plus the additive effect of the interaction between ant exclusion and forest cover at the 2 km-level (Figure 5, Table 3, Table S 3). In landscapes with less than 35% of forest cover, CBB infestation was higher when ants were excluded. At 35% of forest cover, CBB infestation was indifferent to the exclusion of ants, and above 35% this relationship inverted. Meaning, as forest cover increased, CBB infestation increased in the presence of ants and decreased in the exclusion of ants (Figure 5 A). Additionally, in ant exclusions, CBB infestation per branch increased slightly as the distance to the nearest forest fragment increased ($p < 0.001$). While in the presence of ants, CBB infestation decreased rapidly and non-linearly as the distance to the nearest forest fragment increased. As a result, after 25 m of a forest fragment, CBB infestation was lower in the presence of ants ($p < 0.001$, Figure 5 B). The adjusted deviance of this model explained 37% of the variance by the data. The residuals of the model plotted against its fitted values were well distributed. There was only a slight conic-like tendency in the distribution, however there was the same amount of negative and positive values and they adjusted well to a normal distribution, only a minority of points did not fit this inclination.

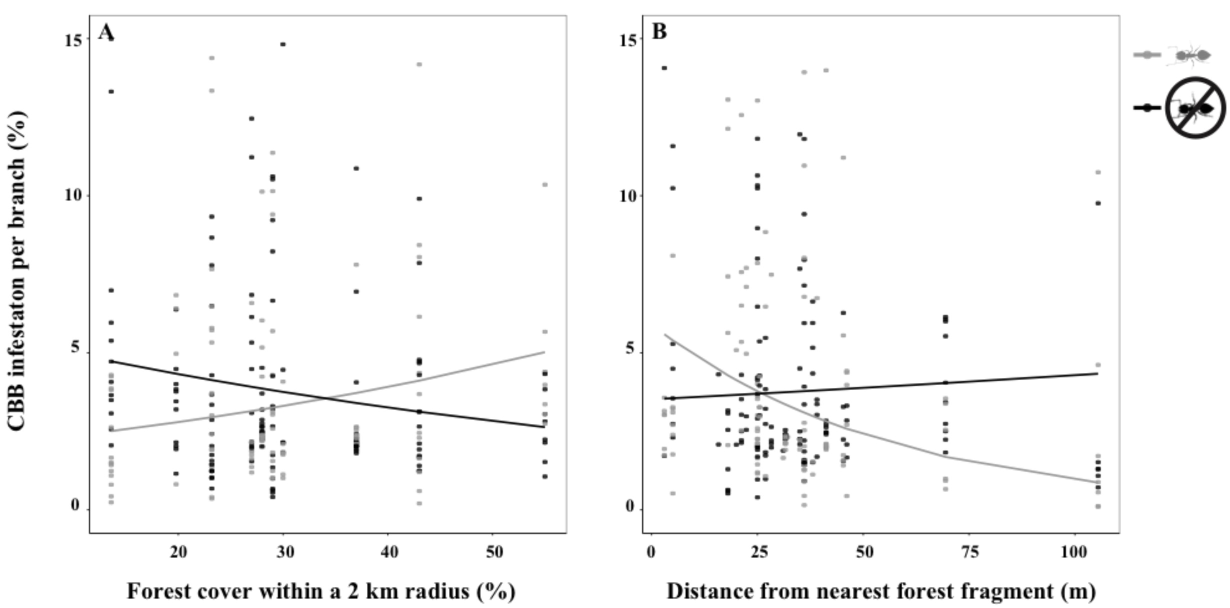

Figure 5. *CBB infestation* percentage per branch in response to an addition of the significant interactions between ant exclusion and forest cover (2 km-level) (A) and ant exclusion and distance to the nearest forest fragment (B).

Table 3. Model (GLMM) results for the fixed effects of ant exclusion and landscape variables on *CBB infestation* per branch (n = 254, df = 9).

Fixed effect	Estimate	Std. error	2.5%	97.5%	*p*
Distance to the nearest forest fragment	-0.36	0.21	-0.79	0.09	0.08
Forest cover (2 km)	0.19	0.43	-0.75	1.12	0.67
Control (presence of ants)	-3.37	0.46	-4.39	-2.43	< 0.001
Treatment (ant exclusion)	-3.25	0.46	-4.26	-2.28	< 0.001
Distance to nearest forest fragment: Treatment (ant exclusion)	0.40	0.08	0.25	0.56	< 0.001
Forest cover (2 km) : Treatment (ant exclusion)	-0.34	0.09	-0.53	-0.16	< 0.001

Percentage of CBB damage per coffee bean

Model selection analysis for bean damage directly in bored berries predicted a model with the addition of two significant interactions between two of the explanatory variables. This model included the addition of an interaction between ant exclusion and forest cover at the 2 km-level and an interaction between ant exclusion and coffee cover at the 300 m-level (Figure 6, Table 4, Table S 4). In ant exclusions, CBB damage per bean decreased drastically as forest cover increased ($p < 0.001$). On the other hand, it was maintained along the forest cover gradient in the presence of ants. Landscapes with less than ~ 35% of forest cover at the 2 km-level had significantly more percentage of CBB damage per bean in the exclusion of ants. Nevertheless, landscapes with more than 35% of forest cover had less CBB damage per bean in the exclusion of ants (Figure 6 A). In addition, in response to coffee cover at the 300 m-level, CBB damage per coffee bean was always significantly higher in exclusion rather than in the presence of ants. In exclusion of ants, we found higher CBB damage as coffee cover increased ($p < 0.001$). However, in the presence of ants, CBB bean damage was retained in the same proportion along the coffee cover gradient (Figure 6 B). The adjusted deviance of this model explained around 25% of the variance by the data. The residuals of the model plotted against its fitted values were well distributed and they adjusted well to a normal distribution.

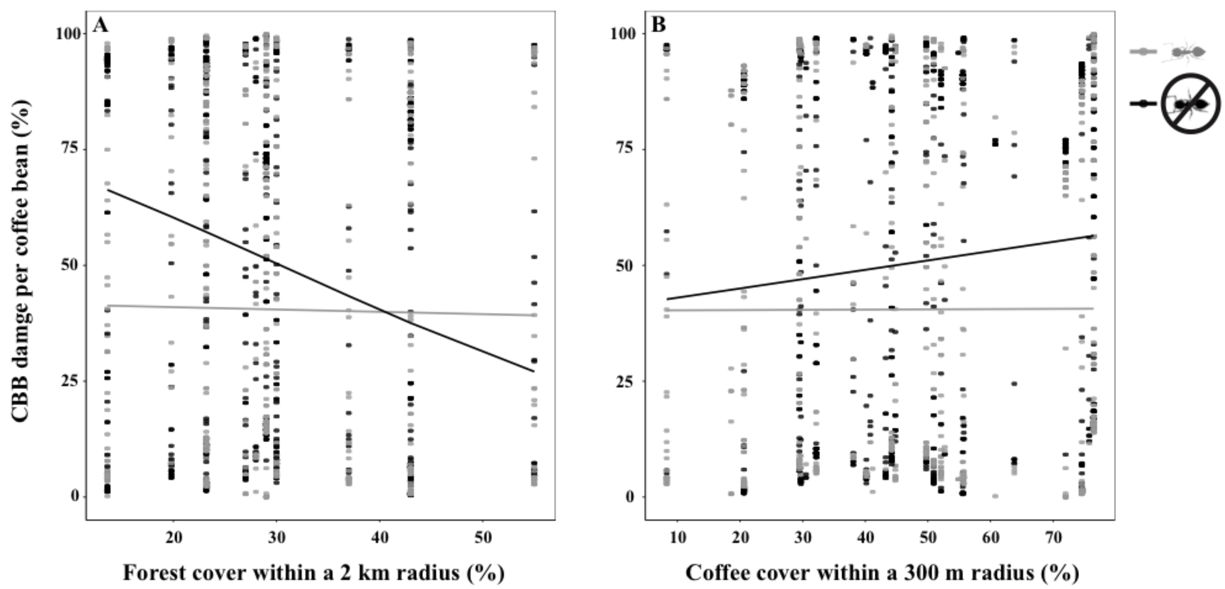

Figure 6. *CBB damage* percentage per infested coffee bean in response to an addition of the significant interactions between ant exclusion and forest cover (2 km-level) (A) and ant exclusion and coffee cover (300 m-level) (B).

Table 4. Model (GLMM) results for the fixed effects of ant exclusion and landscape variables on *CBB damage* per infested coffee bean (n = 2078, df = 8).

Fixed effects	Estimate	Std. error	*p*
Forest cover (2 km)	-0.02	0.14	0.89
Coffee (300 m)	0.00	0.19	0.98
Control (presence of ants)	-0.38	0.16	0.02
Treatment (ant exclusion)	0.03	0.16	0.84
Forest cover (2 km) : Treatment (ant exclusion)	-0.37	0.03	< 0.001
Coffee (300 m) : Treatment (ant exclusion)	0.16	0.03	< 0.001

Discussion

This study presents new evidence that ants are efficient providers of CBB control in sun coffee landscapes and that this ecosystem service is influenced by landscape structure. CBB control is maintained regardless from its proximity to forest fragments, but increases after 25 m. Furthermore, pest control provided by ants is more efficient when coffee cover at the 300 m-level is low, and forest cover at the landscape level (2 km) is below 35%. Contrary to what we expected, forest at the 300 m-level is apparently not affecting the processes involved in this system.

Proximity to forest fragments and pest control of CBB by ants

Proximity from forest fragments is usually related to an increase in pest control services, mainly due to spillover edge effects (Boesing, Nichols & Metzger 2016; Rand, Tylianakis & Tscharntke 2006). In our study, distance to the nearest forest fragment was associated with an increase in CBB presence. Along the distance gradient of our experiments (0–100 m), CBB presence was always between two and three times higher in exclusion of ants. This means ants actually guard coffee plants (or other resources on coffee branches), and prevent CBB from colonizing coffee berries (Perfecto & Vandermeer 2006). Additionally, as we predicted, both in exclusion and presence of ants, CBB presence increased with distance from the nearest forest fragment. It seems that the contributions of ants to prevent CBB from colonizing a coffee berry are stronger near forest fragments, suggesting there could be a spillover process involved. Hence, more CBB predator ant species that cannot otherwise forage directly or solely in distant coffee crops come from nearby forest fragments to patrol CBB colonization. This has also been seen in empirical studies testing prey removal rates in coffee agroecosystems in sun coffee farms in Kenya, where pest removal decreased as distance to the forest fragment increased (Milligan *et al.* 2016).

Distance to the nearest forest fragment was also correlated with a decrease in CBB infestation per branch in the presence of ants, puzzling our predictions. Instead, similarly to our expectations, CBB infestation in the exclusion of ants slightly increases as distance increases. This means that farther away from forest fragments, inside the coffee matrix where CBB are still sprouting, ants are significantly important to control CBB infestation. CBB removal has been found in Kenyan sun coffee landscapes to decrease as distance from forest fragments increases (Milligan *et al*. 2016). More precisely, pest removal was lowest after 25 m from the forest edge (Milligan *et al.* 2016). Perplexing but interestingly, our study found that CBB infestation decreased in the presence of ants specifically after 25 m from the forest edge.

Nonetheless, this result (the maintenance of the service independently of distance) means that the mechanism behind CBB infestation control could be other than prey removal. For instance, there are known mutually beneficial associations between ants and scale insects (*Coccus viridis*, Coccidae) in coffee crops. Perfecto & Vandermeer (2006) found an inversely proportional amount of scale insects and bored berries linked to activity of ants per coffee plant. Additionally, distance from forest fragments is also a significant predictor of ant species richness in habitats of low quality (non-shaded coffee crops). Perfecto & Vandermeer (2002) and Armbrecht & Perfecto (2003) found decreasing species richness as the distance from forest increased. Additionally, Perfecto and collaborators found fewer ant species richness in low quality habitats compared to forest fragments, but the opposite comparing shaded coffee crops to forest fragments. Our landscapes could represent "low quality habitats" (sun coffee monocultures). Accordingly, we could also expect low diversity of ants controlling CBB. However, ant species richness has not been consistently an important factor predicting prey removal in coffee farms (De la Mora, Livingston & Philpott 2008; De la Mora, García-Ballinas & Philpott 2015; Milligan *et al.* 2016). In cacao systems, for instance, exposure of fake caterpillars (prey) showed predation activity was strongly and positively correlated to abundance of the most recorded bird, and not to bird species richness (Maas *et al.* 2015). This could also be the case in our study, where fewer but abundant species are capable of maintaining populations away (more than 25 m) from forest fragments, are adapting well to the coffee matrix, and are providing CBB control efficiently.

Coffee cover and pest control of CBB by ants

CBB presence was additionally explained by the amount of coffee cover as observed in other studies (Avelino *et al.* 2012; De la Mora, García-Ballinas & Philpott 2015). CBB presence was higher in ant exclusions at least until 65% of coffee cover in a radius of 300 m. Throughout the entire field season, we observed ants actively nesting and foraging in coffee crops. Some of the most commonly observed ant species belong to the genera *Linepithema*, *Pheidole, Solenopsis, Crematogaster*, *Camponotus*, *Neoponera*, and *Brachymyrmex*, which were also found to be associated with coffee agroecosystems in previous studies (Armbrecht & Perfecto 2003; Armbrecht & Gallego 2007; Perfecto & Vandermeer 2002, De la Mora & Philpott 2010). Ants from these genera are associated to open and disturbed habitats and are omnivorous generalists (Fernández 2003). In our study, these ants were observed using fallen coffee branches, hollow twigs, and coffee trunks to nest and coffee branches and leaf litter to forage, among other resources normally found in coffee agroecosystems. In a Mexican study, ants removed more CBB as rustic coffee cover increased (in a 200 m-level), and with more number of coffee plants (De la Mora, García-Ballinas & Philpott 2015). De la Mora, García-Ballinas & Philpott (2015) also found more CBB removed by ants with increasing number of hollow twigs. However, in our study, as coffee cover increased, the probability of CBB presence increased as well. Coffee expansion is either deteriorating pest control by ants or positively affecting the abundance of agricultural pests (Avelino *et al.* 2012). For instance, Avelino and collaborators (2012) showed that increments in coffee cover increase the abundance of CBB and other coffee pests such as coffee leaf rust and coffee root-knot nematodes.

The amount of coffee cover was also an important explanatory variable to explain CBB bean damage. CBB damage resulted higher in ant exclusions in association of the amount of coffee cover in a radius of 300 m. Meeting our expectations, the differences in pest control between exclusion and presence of ants increased for CBB bean damage as coffee cover increased, which corroborates CBB bean damage as being suppressed in the presence of ants. Increase of coffee cover at local levels (200–300 m around coffee trees) has also been an important factor in predicting prey removal of coffee pests by ants (De la Mora, García-Ballinas & Philpott 2015). Ant genera related to this type of pest control (i.e. *Linepthema*, *Pheidole*, *Solenopsis)*, are generalists, aggressive, abundant, and usually favored by human-disturbed habitats (Fernandéz 2003). In our study, coffee expansion hints to varied effects of pest control services by ants. Specifically, as coffee cover increased there was a decrease in pest control for CBB presence probability and an increase in pest control for CBB bean damage.

Forest cover and pest control of CBB by ants

CBB infestation and damage were explained by the amount of forest cover at the 2 km-level. The relationships among ants, CBB infestation, and forest cover were different and more complex than what we predicted. Landscapes with at least 35% of forest cover resulted with higher CBB infestation percentages in ant exclusions, while landscapes with more than 35–40% forest cover showed an inverted pattern, with less CBB infestation in the exclusion of ants. Meaning, landscapes benefit most from pest control provided by ants in landscapes with 35–40% forest cover (2 km-level). This is paradoxical and counterintuitive to our predictions. Interestingly, after this point, CBB infestation is lower in the exclusion of ants. Meaning possibly, that other organisms that also contribute with CBB control (i.e. insectivorous birds) benefit from high percentages of forest cover (Karp *et al.* 2013). The integrity of bird communities in the Atlantic Forest recover and stabilize in landscapes with more than 35–40% of forest cover (Banks-Leite *et al.* 2014). Also, interactions among different functional guilds (natural enemies with common prey such as flying insects, ground-dwellers, and vertebrates) have negative impacts on pest control with increasing landscape complexity, or >25% semi-natural habitat (Martin *et al.* 2013). Therefore, as forest cover increases in our study, predatory pressures on ants also increase. This is reflected in less success of CBB infestation control by ants after ~ 35% of forest cover, while CBB infestation continues to decrease as forest cover increases in the exclusion of ants.

Furthermore, ants and forest cover (2 km-level) were important in this study to prevent CBB bean damage. In the presence of ants, CBB bean damage remains stagnated. This means that independently of the process behind arrival of CBB, once it colonizes, ants contribute to control CBB damage directly in coffee beans. Additionally, as we predicted, in ant exclusions, CBB damage strongly decreases as forest cover (2 km-level) increases. Specifically, CBB bean damage is lower in landscapes with more than 35–40% forest cover. In this case, pest control provided by ants is benefited in landscapes with higher amount of forest cover. It is almost a complementary trade-off, landscapes with > 35% forest cover will have more predatory pressure on ants (lowering their CBB infestation control), however increasing CBB bean damage control. It is as if in the exclusion of ants, once CBB is inside a coffee berry where it can no longer be predated by birds (or other bigger natural enemies), ants are even more important CBB control providers. Using percentage of bean damage by CBB as an indicator of CBB pest control is not common in the literature. Nevertheless, it turned out to be fundamental in better understanding this system since it shows that pest control provided by ants does not stop at weakening CBB colonization and infestation. It continues by obstructing CBB damage directly in infested coffee berries, which is ultimately what will bring profit to farmers. Based on our results, this step further of pest control is actually provided by ants. Especially because some of the most common ant species observed during our field season, such as *Linepithema*, *Pheidole*, *Solenopsis*, are small enough to fit through holes made by CBB and could potentially predate CBB inside coffee berries. Individuals from the genus *Solenopsis* were found in several occasions inside bored coffee berries (authors' observations).

On the other hand, forest cover at the local level (300 m) was not an important predictor of CBB control provided by ants. This is opposite to our expectations and to previous findings (De la Mora, Murnen & Philpott 2013). We think that forest cover in general (at small and large scales) can be influencing processes that include a temporal component through more than one coffee production season. Forest fragments could be sources of ants and other CBB predators to repopulate the coffee matrix after being diminished by general pesticides. Ants are frequently confronted with pesticides meant for other pests in this region and with targeted insecticides because ants are commonly perceived as pests themselves (Philpott & Armbrecht 2006). Therefore, forest cover at small scales (300-m level) must be particularly important considering ants usually fly short distances in their nuptial flights, which is their main migratory event (Hölldobler & Wilson).

Implications for coffee landscape management

This study highlights the significance of ants in CBB pest control reducing CBB presence, infestation and bean damage in sun coffee landscapes. Moreover, this study accentuates the importance of attention to land use and the composition and configuration within agricultural landscapes. CBB control is favored near forest fragments. After 25 m from forest edges, ants are not only regulating CBB presence, but also and mainly avoiding CBB infestation. Also, it would seem that ~ 35% of forest cover (2 km-level) is a mixed threshold after which pest control by ants for CBB infestation decreases and for bean damage increases.

Likewise, this study conveys new information to design multifunctional landscapes in one of the most economically important regions for coffee production. These recommendations include reduction of coffee cover locally (300 m-level) or lessening extension of coffee crops by increasing the proximity of forest fragments to coffee lines until at least 25 m from a forest edge. Consequently, the probability of CBB presence could be reduced almost by half and infestation per branch nearly by 5%. Guaranteeing at least 35% of forest cover in a radius of 2 km around coffee crops will maintain coffee branches with at least ~ 2% less CBB infestation and decrease bean damage by ~ 25%.

We recommend the incorporation of forest fragments within the coffee matrix as sources of natural enemies. They could potentially provide pest control in the adjacent coffee systems and minimize negative effects of the transformation of forests into agricultural landscapes (Landis, Wratten & Gurr 2000). The majority of pest control providers are mobile organisms that should benefit from the addition of forest fragments locally and at the landscape scale. Additionally, forest cover offers habitat and other resources for ants and other providers of pest control (i.e. insectivorous birds) throughout the year (Boesing, Nichols & Metzger submitted) when coffee berries are not developed. This could be especially true because coffee trees are trimmed and cut to re-grow in this region typically every two and seven years, respectively. Furthermore, we highly recommend a change of paradigm in the perception of coffee landscapes as "low quality habitats" towards habitats that sustain ecological processes capable of providing pest control and other ecosystem services. This final point deserves further attention and exploration. We believe, as well, that it is a key step in order to bridge the gap between conservation and coffee production in fragmented landscapes (Perfecto & Vandermeer 2002; Vandermeer & Perfecto 2007; Tscharntke *et al.* 2012).

Perspectives

We recognize that there is a long way until "optimal" designs are reached for coffee agroecosystems and completely multifunctional landscapes. For instance, CBB presence, or colonization, is also affected by other factors not tested in this study, such as humidity, local temperature, and preceding farm management (i.e. sweeping fallen or old coffee berries off the ground post-harvesting). We advise incorporating these variables as local factors in future studies. Also, it seems from this study that we are observing different landscape (possibly cross-boundary spillover effects) and ecological effects acting on CBB, ants, and on other providers of CBB control who also predate on ants (possibly insectivorous birds). An increment of forest cover within the matrix will additionally connect forest remnants (Avelino *et al.* 2012), but it is recommended for future studies, to include more variables that measure connectivity processes and the quality of the matrix (Boesing, Nichols & Metzger submitted). Also, we recommend the inclusion of data on the ecological role of other organisms also involved in coffee agroecosystems because provision of ecosystem services is mostly the result of interaction networks and not individual species.

Conclusion

Sun coffee matrices are usually considered “low-quality habitats” and sometimes even disregarded for provision of ecosystem services. We show here that this is not the case at all. Coffee farmers benefit from CBB control by ants within these coffee landscapes. CBB presence, infestation, and bean damage are lessened in the presence of ants in interaction with the surrounding landscape structure.

We found higher chances of CBB colonization as distance from the nearest forest fragment increased. Forest remnants in coffee landscapes most probable serve as source populations which consequently, spillover to adjacent agricultural matrices. Hence, providing natural enemies that offer pest control services, through propagation of ants that predate or remove CBB. This could be achieved either throughout temporal processes that repopulate agricultural systems when ant populations decrease, or throughout spatial processes foraging from nearby forest fragments.

Control of CBB infestation however, is provided independently from the distance to the nearest forest fragments, but is accentuated beyond 25 m. Consequently; we believe abundant and common species of ants, key providers of CBB control, are adapted to the matrix in sun coffee farms. Similarly, expansion of coffee cover increases CBB colonization, but support control of CBB bean damage by ants. However, conservation of at least 35% of forest cover in landscapes within 2 km radius promote reduction of CBB infestation and bean damage by ants.

Landscapes with higher levels of forest cover, are apparently also benefiting with CBB control by other organisms (i.e. insectivorous birds). Altogether, these results allow us to propose some landscape management recommendations that can not only contribute in the perpetuation of CBB control by ants in coffee farms, but also in the protection or restoration of Atlantic Forest remnants for the benefit of all.

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Supplementary material

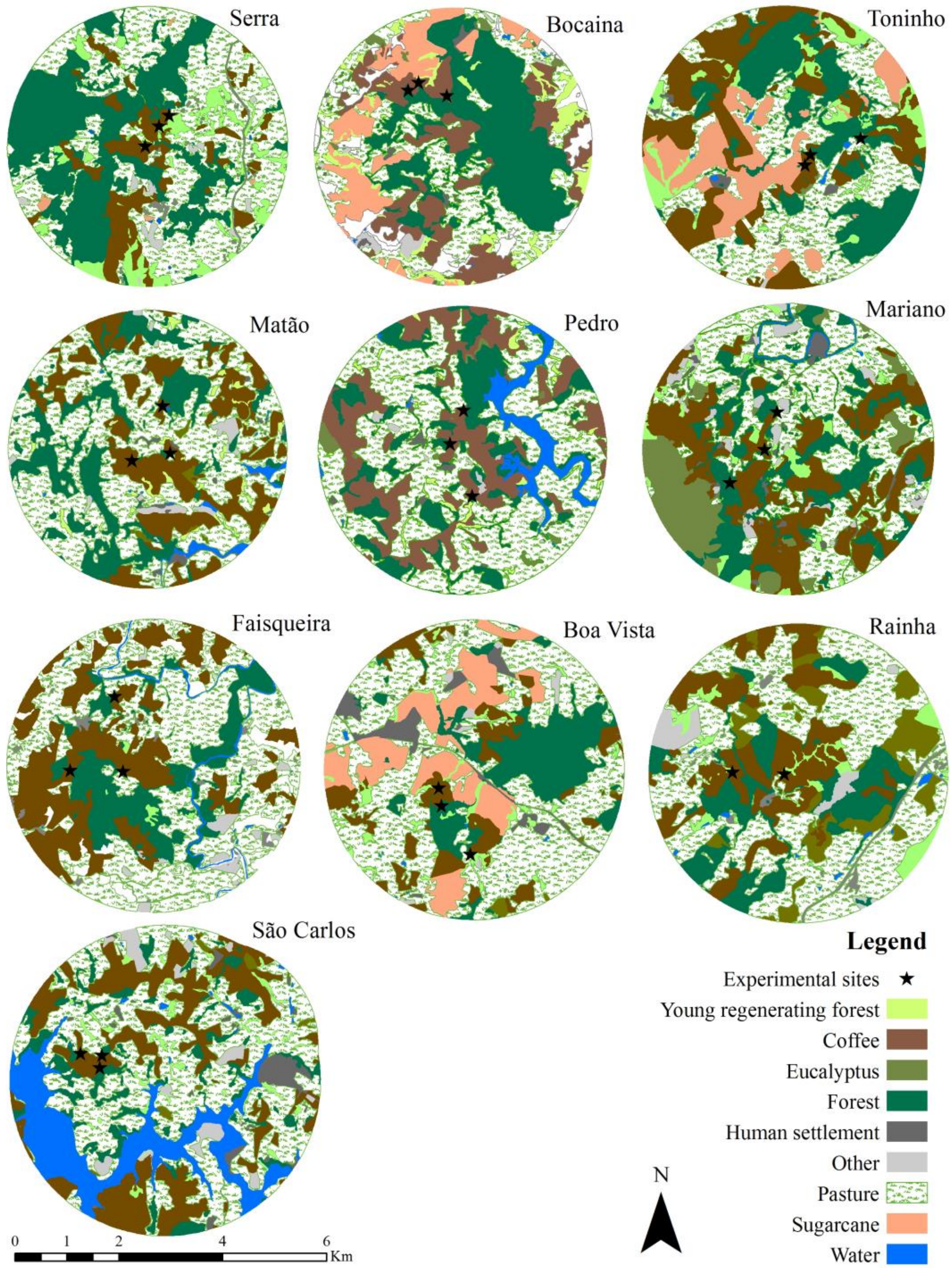

Figure S 1. Land use within each landscape (with a radius of 3 km) included in the study. For geographical locations and other attributes see Table S 1.

Figure S 2. Ant exclusion experiment by the application of Tanglefoot Insect Barrier. Notice the isolation of the branches of interest, marked with blue ribbons.

Table S 1. Extension of land-uses (%) for the 10 landscapes included in the study, each with a total of 2830 ha in a radius of 3 km.

Landscape	Forest	Coffee	Young regenerating forest	Eucalyptus	Pasture	Water	Human settlement	Sugarcane	Other	Central geographical location	
										Latitude	Longitude
Serra	34	11	7	0	45	0	1	0	1	-21° 54'	-46° 43'
Bocaina	30	17	6	1	24	0	1	12	9	-21° 20'	-46° 40'
Toninho	23	24	7	0	30	0	1	15	0	-21° 25'	-46° 42'
Matão	20	25	2	1	47	2	2	0	2	-21° 42'	-46° 36'
Pedro	18	27	3	12	33	1	3	0	3	-21° 46'	-46° 27'
Mariano	18	23	2	1	48	6	1	0	1	-21° 41'	-46° 32'
Faisqueira	16	12	3	1	46	0	5	16	1	-21° 29'	-46° 42'
Boa Vista	16	26	0	6	45	2	2	0	2	-21° 43'	-46° 28'
Rainha	16	20	4	10	43	1	2	0	3	-21° 47'	-46° 40'
São Carlos	9	23	2	1	42	16	3	0	3	-21° 38'	-46° 32'

Table S 2. Model (GLMM) results for the random effects of ant exclusion and landscape variables on *CBB presence* per branch (n = 539, df = 8).

CBB presence random effects	Groups	Variance	Std. Dev.
Landscape ID : Site ID : Plant ID	270	0.16	0.40
Landscape ID : Site ID	27	1.49	1.22
Landscape ID	10	0.00	0.00

Table S 3. Model (GLMM) results for the random effects of ant exclusion and landscape variables on *CBB infestation* per branch (n = 254, df = 9).

CBB infestation random effects	Groups	Variance	Std. Dev.
Landscape ID : Site ID : Plant ID	174	0.89	0.94
Landscape ID : Site ID	27	0.56	0.75
Landscape ID	10	1.70	1.30

Table S 4. Model (GLMM) results for the random effects of ant exclusion and landscape variables on *CBB damage* per coffee bean (n = 2078, df = 8).

CBB damage random effects	Groups	Variance	Std. Dev.
Landscape ID : Site ID	27	0.64	0.80
Landscape ID	10	0.00	0.00

General Conclusions

Coffee agroecosystems previously perceived as “low quality habitats,” could be known now as landscapes that provide pest control services. Atlantic Forest fragments are sources of natural enemies of one of the worst coffee pests, the coffee berry borer (CBB). We identify ants that provide CBB control in Brazilian sun coffee farms. Moreover, we better understand how this regulatory ecosystem service is modulated by the landscape composition and configuration in highly fragmented systems.

We showed with this study that proximity to forest fragments prevents CBB colonization. However, CBB infestation control is maintained regardless of the distance to the nearest forest fragment. There is a trade-off in pest control services provided by different species according to the amount of forest cover at the landscape level (2 km): low amounts (< 35%) support the control of CBB infestation and bean damage by ants, but high amounts (> 35%) probably benefit other organisms (i.e. insectivorous birds), who control CBB but also predate on ants, reducing the contribution of ants towards CBB control. Meaning possibly that 35% is a threshold in this Atlantic Forest system and deserves further attention. On the other hand, forest cover at the local level (300 m) did not reflect any direct effects in these processes, but we hypothesize forest cover could be involved indirectly in processes not measured in this study. Additionally, amount of coffee cover at the local level (300 m) has a strong direct effect increasing CBB presence and an inverse effect reducing CBB bean damage.

We suggest that addition of forest cover within the coffee matrix will have a double beneficial effect. First, it will decline expansion of coffee cover associated with increments of presence of CBB. Second, it will maintain enough levels of forest cover to sustain natural enemies of CBB, such as ants, insectivorous birds or others. Furthermore, we recommend a change in the perception of the coffee matrix and the incorporation of the matrix in landscape planning. The coffee matrix should be considered a habitat that involves ecological processes capable of providing CBB control and other ecosystem services by ants and other organisms.

This study makes part of Project Interface, a composite research project that aims to better understand the ecological processes and mechanisms involved in multiple ecosystem services and the relationships involved with landscape structure. Eventually, this project aims to contribute to plan and design multifunctional landscapes capable of improving agricultural productivity and protecting biodiversity and the ecosystem services they provide. Therefore, in this context, this dissertation contributes toward a better design for coffee agroecosystems that allow and enhance CBB control, lessen dependence on pesticides, and encourage conservation or restoration of forest fragments within the coffee matrix. We suggest further studies should consider and evaluate data for matrix quality, connectivity processes and the interaction network of other providers of ecosystem services.