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Ant-mediated (Hymenoptera: Formicidae) biological control of the coffee berry borer: diversity, ecological complexity, and conservation biocontrol

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Abstract

Ants are important biological control agents of the coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari, 1867), the most damaging insect pest of coffee around the world. Ants also occur naturally in coffee landscapes, opening the door to conservation biocontrol approaches, which can promote both biodiversity conservation and crop production. Here, we review evidence that shows that ants antagonize and predate CBB, reduce CBB infestation, and contribute to the suppression of CBB populations. We discuss the potential mechanisms and impacts of ant diversity and interaction complexity on the functioning of CBB biocontrol. We also discuss the implications of conservation biocontrol in coffee farm management, reviewing literature showing that ant communities and CBB respond to coffee farm intensification and the composition of the agricultural matrix. We assess the potential impacts of ant-CBB biocontrol on coffee production and yield, considering the complexities that result from promoting diverse ant communities in conservation biocontrol, and discuss potential disservices of ants. Finally, we end with several research avenues that are needed to further illuminate the overall role of ant communities on coffee pests and yield and to make specific recommendations for ant-CBB biocontrol management.

Spanish abstract

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Key words: Coffee, coffee berry borer, conservation biocontrol, biodiversity, interaction complexity, review.

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Introduction

Globally, agricultural intensification is one of the most significant drivers of habitat degradation and, subsequently, biodiversity declines. Nearly 40% of earth's terrestrial surface is under agricultural production (Foley & al. 2011). Agroecological strategies that integrate both conservation and crop production are increasingly necessary (Kremen 2015). Conservation biocontrol is an approach which aims to bolster naturally occurring enemy communities through the maintenance of habitat, in and around farms, so they may better control pests and may have the benefit of conserving additional biodiversity in the process (Barbosa 1998). This approach can be more effective than classical biocontrol because the natural enemies promoted are typically generalists, which persist in the field even when pest populations are low and may also predate secondary pests (Symondson & al. 2002). Additionally, diverse natural enemy communities may be more robust to environmental disturbances and future pest outbreaks (Straub & al. 2008, Crowder & Jabbour 2014). However, whether natural enemy diversity benefits pest control is context-dependent (Letourneau & al. 2009) and is driven by complex interactions between natural enemy species (Straub & al. 2008, Crowder & Jabbour 2014) and the ecological networks (Vandermeer & al. 2010, Wielgoss & al. 2014) in which they are embedded.

Coffee is an important global agricultural commodity – more than one billion cups of coffee are consumed every day (Jha & al. 2014). Over 20 million farming families grow coffee in some 80 countries around the world and are dependent on its production for their livelihoods (Vega & al. 2003, Donald 2004, Vega & al. 2015). Most coffee production occurs in biodiversity hotspots in the tropics – areas known for their conservation importance (Moguel & Toledo 1999). Coffee farms and landscapes can provide habitat for an impressive array of biodiversity (Perfecto & al. 1996, Perfecto & al. 2005, Philpott & al. 2008a, Jha & al. 2014). However, coffee intensification, through the removal of shade-trees and increased use of agrochemicals, reduces biodiversity on farms (Philpott & al. 2008a, Perfecto & Vandermeer 2015). Furthermore, both planned and associated biodiversity on coffee farms contributes to important ecosystem services, including pest control (Vandermeer & al. 2010, Jha & al. 2014). Coffee systems are therefore well-suited for the implementation of agroecological practices, such as conservation biocontrol, to promote both conservation and production (Perfecto & Vandermeer 2015).

The coffee berry borer (CBB) (*Hypothenemus hampei* (Ferrari, 1867), Coleoptera: Curculionidae), is one of the most economically devastating pests of coffee around the world (Damon 2000, Jaramillo & al. 2006). This small beetle specializes on the fruits of both commercial species of coffee, *Coffea arabica* and *Coffea canephora* (*robusta*), for its reproduction and growth. Upon colonization of a coffee plant after dispersal, mature female CBB bore gallery tunnels into fruits, where they lay their eggs. After the CBB eggs hatch, the larvae consume the endosperm of the fruit where they complete their development until they are ready to colonize new fruits (Damon 2000). Infestation damages the fruit through direct consumption by the borers and by facilitating the infection of saprophytic microorganisms which deteriorate the coffee bean (Damon 2000). This damage reduces the quality of the coffee crop, and in the worst cases can lead to early fruit senescence and complete degradation of the berry. CBB is now nearly ubiquitous in coffee producing regions, with infestation levels in some cases at 100% of fruits, and the highest yield losses ranging from 35% to 80% (Vega & al. 2015). It is estimated that this damage costs farmers over $500 million (U.S. dollars) in yield losses annually (Vega & al. 2015), with additional expenses in the cost of pesticides used to control it.

The literature on CBB is extensive (Pérez & al. 2015) and a range of control strategies have been identified with various levels of potential effectiveness and implications for agroecological sustainability (Murphy & Moore 1990, Damon 2000, Bustillo & al. 2002, Jaramillo & al. 2006, Vega & al. 2009, Vega & al. 2015, Aristizábal & al. 2016). Manual or cultural control, where farm workers make multiple passes during harvest to clean plants of all unpicked berries can help to reduce resources for the borer in-between growing seasons (Damon 2000). This, however, requires increased on-farm labor, and is often ineffective as many fruits that fall to the ground are missed and serve as reservoirs of CBB for the next season (Baker & Barrera 1993). In intensified coffee production, pesticides, such as endosulfan, are used to control CBB, but with limited success. Because the borer spends the majority of its life cycle inside of berries, it is mostly protected from surface-applied chemicals (Damon 2000, Vega & al. 2009). However, when borer populations are reduced by endosulfan, resistance can spread rapidly (Brun & al. 1989, Vega & al. 2015). These shortcomings, combined with the high toxicity of endosulfan and other pesticides, have made chemical control suboptimal (Jaramillo & al. 2006).

Due to the difficulties of manual and chemical control of CBB, much attention has been given to the potential biological control of this pest. Most of this discussion has focused on classical and augmentation biological control strategies, where enemies are reared and then released on farms to reduce CBB populations (Jaramillo & al. 2006, Vega & al. 2009). Among the commonly used classical biocontrol agents are several wasp parasitoids, mostly native to central Africa where the CBB originated, and the fungal entomopathogen *Beauveria bassiana* (although this often occurs naturally, its presence can be augmented by spraying fungal spores on plants). While classical biocontrol can be an effective means of sustainable pest control, results with CBB have been limited, and the rearing and release of natural enemies can be costly and labor-intensive (Vega & al. 2015). Furthermore, classical biocontrol risks that introducing novel organisms into systems can result in unintended invasions and the disruption of interaction networks (Simberloff & Stiling 1996, Simberloff 2012).

Conservation biocontrol, in contrast, is a promising pest control approach in coffee. Recent research has demonstrated that native generalist predators, like birds, can significantly reduce CBB infestation and prevent yield loss, when they are bolstered by the conservation of near-by forest patches (Kellermann & al. 2008, Johnson & al. 2010, Karp & al. 2013). Ants also occur naturally in coffee and act as important natural enemies of CBB, yet are underrepresented in the general CBB biocontrol literature (Murphy & Moore 1990, Damon 2000, Bustillo & al. 2002, Jaramillo & al. 2006, Vega & al. 2009, Aristizábal & al. 2016). Some research also suggests a low awareness of ants as natural enemies of CBB by coffee farmers in Latin America, despite concerns about CBB by both organic and conventional growers (Segura & al. 2004). This is surprising given the rich history and potential of ants as biocontrol agents in agriculture around the world (Carroll & Risch 1990, Way & Khoo 1992, Perfecto & Castiñeiras 1998, Offenberg 2015). Ants possess unique traits as natural enemies, where colonies can efficiently respond to changes in prey density by varying worker recruitment rates and can consume high numbers of prey without satiating by storing resources (Risch & Carroll 1982, Offenberg 2015). For these reasons, ants are used for biocontrol in various crop systems throughout the world, ranging from cotton to cocoa, citrus, coconut, sweet potato, and maize-wheat systems (Perfecto & Castiñeiras 1998). Indeed, their use in citrus groves in China dates back hundreds of years (Huang & Pei 1987).

Here, we review research on the potential of ant-mediated biological control of the coffee berry borer (Tab. 1). We define biological control, generally, to include the suppression of CBB damage, densities, and populations, all of which may indirectly enhance coffee yields. While these forces may not always work to reduce CBB infestation below economic thresholds on farms, we assume that they contribute to the overall regulation of CBB populations and are therefore providing an important ecosystem service. We approach this subject from a conservation biocontrol perspective, where we examine the potential of ants as natural control agents in coffee systems and consider agroecological management strategies for promoting ant-mediated CBB biocontrol. We review the potential of individual ant species, but also explore how diverse assemblages of ants embedded in complex ecological networks, as are promoted through conservation biocontrol, contribute to biocontrol function. We review what is known on this subject to assess the overall potential of ant conservation for reducing CBB damage and preventing yield loss in coffee systems. Finally, we highlight gaps in knowledge for future research, so that farmers may have the full set of tools available to them in making decisions about sustainably managing for ants in the control of CBB on their farms.

Ant-mediated biological control of the coffee berry borer

Ant communities in coffee agroecosystems are generally diverse, where species can be classified into several foraging and nesting groups. We focus our discussion of ants based on their potential interactions with CBB to two general

Tab. 1: Primary literature on the potential of ants as biological control agents of the coffee berry borer. The type of study is noted, where (l) indicates laboratory and (f) indicates field. Some non-refereed reports were included and are indicated with *.

Reference	Region	Method	Species
Leefmans (1923)*	Indonesia	Experiment (f)	*Dolichoderus bituberculatus*
Fonseca & Araujo (1939)*	Brazil	Observation (f)	*Crematogaster curvispinosa*
Bustillo & al. (2002)	Colombia	Observation (f)	*Brachymyrmex* sp., *Crematogaster* sp., *Paratrechina* sp., *Pheidole* sp., *Prenolepis* sp., *Solenopsis* sp., *Wasmannia* sp.
Infante & al. (2003)	Mexico	Observation (l)	*Tapinoma* sp.
Armbrecht & Perfecto (2003)	Mexico	Observation (l)	*Crematogaster* sp., *Pheidole* sp., *Solenopsis* spp. (2)
Varón & al. (2004)	Costa Rica	Experiment (f)	*Crematogaster crinosa*, *Pheidole radoszkowskii*, *Solenopsis geminata*
		Experiment (l)	*Crematogaster crinosa*, *Crematogaster curvispinosa*, *Crematogaster torosa*, *Pheidole radoszkowskii*, *Solenopsis geminata*
Gallego Ropero & Armbrecht (2005)	Colombia	Experiment (f)	Tested general ant community effects
		Experiment (l)	*Solenopsis picea*, *Tetramorium simillimum*
Perfecto & Vandermeer (2006)	Mexico	Correlation & Experiment (f)	*Azteca sericeasur*
Vázquez Moreno & al. (2006)	Cuba	Observation (f)	*Pheidole megacephala*, *Pseudomyrmex* sp., *Solenopsis geminata*, *Wasmannia auropunctata*
Vélez & al. (2006)	Colombia	Experiment (f)	Tested general ant community effects
Armbrecht & Gallego (2007)	Colombia	Experiment (f)	Tested general ant community effects
		Experiment (l)	*Paratrechina* cf. *steinheili*, *Solenopsis* cf. *picea*, *Tetramorium simillimum*
Vera-Montoya & al. (2007)	Colombia	Experiment (l)	*Crematogaster* sp.
Philpott & al. (2008d)	Mexico	Experiment (f)	Tested general ant community effects
Vázquez Moreno & al. (2009)	Cuba	Correlation (f)	*Monomorium floricola*, *Pheidole megacephala*, *Solenopsis geminata*, *Tetramorium bicarinatum*, *Wasmannia auropunctata*
Larsen & Philpott (2010)	Mexico	Experiment (f)	Tested general ant community effects
		Experiment (l)	*Pseudomyrmex ejectus*, *Pseudomyrmex simplex*, *Pseudomyrmex* sp.
Pardee & Philpott (2011)	Mexico	Experiment (l)	*Azteca sericeasur*
Philpott & al. (2012)	Mexico	Experiment (l)	*Azteca sericeasur*, *Procryptocerus hylaeus*, *Pseudomyrmex simplex*
Gonthier & al. (2013)	Mexico	Experiment (f)	*Azteca sericeasur*, *Crematogaster* spp., *Pheidole synanthropica*, *Pseudomyrmex ejectus*, *Pseudomyrmex simplex*, *Solenopsis picea*, *Tapinoma* sp., *Wasmannia auropunctata*
Jimenez-Soto & al. (2013)	Mexico	Correlation (f)	*Azteca sericeasur*, *Crematogaster* spp., *Pheidole synanthropica*, *Pseudomyrmex simplex*, *Solenopsis picea*
		Experiment (f)	*Azteca sericeasur*, *Pheidole synanthropica*
Trible & Carroll (2014)	Costa Rica	Experiment (f)	Tested general ant community effects
De la Mora & al. (2015)	Mexico	Experiment (f)	Tested general ant community effects
Gonthier & al. (2015) preprint*	Mexico	Experiment (l)	*Azteca sericeasur*, *Pseudomyrmex ejectus*, *Pseudomyrmex simplex*
Morris & al. (2015)	Mexico	Experiment (f)	*Azteca sericeasur*
Morris & Perfecto (2016)	Mexico	Experiment (l)	*Solenopsis picea*, *Wasmannia auropunctata*
Onishi & al. (2017)	Thailand	Experiment (l)	*Camponotus nicobarensis*, *Crematogaster* sp., *Dolichoderus* sp., *Tapinoma* sp., *Technomyrmex modiglianii*, *Technomyrmex yamanei*, *Anoplolepis gracilipes*

foraging guilds: arboreal and ground ants (Perfecto & Vandermeer 2013). Arboreal ants typically nest and forage on shade trees and coffee plants and include twig-nesting, carton nesting, and weaver ants (Philpott & Foster 2005, De la Mora & al. 2013, Gillette & al. 2015). Ground ants typically forage and nest on the ground in soil, leaf litter, twigs and decomposing wood (Armbrecht & Perfecto 2003, Armbrecht & al. 2005, De la Mora & Philpott 2010). Some ant species are generalists in their foraging and nesting habitats and can be found both on the ground and on plants, sometimes at the same site (Perfecto & Vandermeer 2013). Because of the diversity of ant species in these two general guilds, ant-mediated biological control can occur through several mechanisms, where ants can interact with free-roaming CBB and CBB inside berries, both on coffee plants and the ground (Fig. 1).

Infestation suppression on coffee plants: Arboreal ants can potentially contribute to pest suppression through multiple mechanisms, including predation, non-consumptive attacks, and indirect chemical deterrence (Way & Khoo 1992).

Arboreal ants readily forage and tend hemipteran insects in coffee plants, often maintaining high activity levels near berries on branches. This provides a window of opportunity to interact with adult CBB individuals as they colonize coffee berries (Fig. 1a). A number of studies provide evidence that these species can reduce the level of CBB infestation (percentage of bored berries) on coffee plants in farms. Several field studies have correlated ant presence on coffee plants with CBB infestation. In Mexico, the keystone ant species *Azteca sericeasur* LONGINO, 2007 (formerly identified as *A. instabilis* SMITH, 1862) is associated with lower levels of bored coffee fruits (PERFECTO & VANDERMEER 2006). The authors recorded an inverse relationship between the density of green coffee scale (*Coccus viridis* GREEN, 1889), which correlates positively with *A. sericeasur* activity (VANDERMEER & al. 2002), and the proportion of coffee fruits bored. Another study conducted surveys of ants on coffee plants in different farms in Cuba and found a small negative correlation between ant species diversity and borer infestation levels (VÁZQUEZ MORENO & al. 2009). In Mexico, JIMÉNEZ-SOTO & al. (2013) systematically baited for ants in coffee plants, and correlated ant presence and species to CBB infestation. Coffee plants with at least one species of ants present had significantly lower mean infestation (10.6% fewer bored berries) than plants without ants. Plants with either of two dominant ant species, *A. sericeasur* and *Pheidole synanthropica* LONGINO, 2009 had even greater CBB infestation differences than on plants without ants (12.3% and 15.4% fewer bored berries, respectively) (JIMÉNEZ-SOTO & al. 2013). Additionally, CBB gallery lengths were significantly shorter on plants with ants than on non-ant plants, suggesting that the ants attack and remove CBB during the boring process, preventing further damage to the berry. However, when looking at plants by individual ant species, this trend was only observed with *P. synanthropica*.

Several behavioral studies have directly tested CBB removal by ants. PERFECTO & VANDERMEER (2006) placed live adult borers on coffee fruits and measured the amount of time until ants removed them. *Azteca sericeasur* activity correlated positively with CBB removal rates and ants carried the CBB back to their nest nearly half the time, indicating predation (PERFECTO & VANDERMEER 2006). JIMÉNEZ-SOTO & al. (2013) employed the same method with two dominant ant species, but in this case, recorded videos of the ants to analyze their behavior in the presence of CBB. They observed that ants discovered the borers in most cases and proceeded to attack them, however, *A. sericeasur* usually threw CBB off plants, while *Pheidole synanthropica* typically carried the prey back to their nest. The difference in predatory behavior between the ants was attributed to possible variation in their nutritional requirements, which may be driven by differences in the frequency that they tend hemipterans (JIMÉNEZ-SOTO & al. 2013). Ants that aggressively tend and defend hemipterans on plants, like *A. sericeasur*, often exhibit non-consumptive attacks on other herbivores as they patrol plants (Fig. 1c) (WAY & KHOO 1992, PHILPOTT & ARMBRECHT 2006). In another removal study, authors used dead CBB as sentinel prey and documented *P. synanthropica* and at least six other ant species removing individuals from coffee plants (DE LA MORA & al. 2015).

Some studies have conducted manipulative enclosure experiments in the laboratory to isolate the effects of ants on CBB infestation reduction. In Mexico, two studies placed coffee branches with fruits and adult CBB individuals inside mesh cages and measured infestation in the presence and absence of ants after 24 h (PARDEE & PHILPOTT 2011, PHILPOTT & al. 2012). Both found that the arboreal ant *Azteca sericeasur* reduces CBB infestation by ~ 50%, but that the efficiency of the ants drops significantly when they are attacked by phorid parasitoids in the genus *Pseudacteon* introduced into the cages (PARDEE & PHILPOTT 2011, PHILPOTT & al. 2012). PHILPOTT & al. (2012) also showed that two other species of twig-nesting ants, *Pseudomyrmex simplex* (SMITH, 1877) and *Procryptocerus hylaeus* KEMPF, 1951, individually reduced borer infestation by roughly 50% under the same conditions. Another study reported similar results for *A. sericeasur* and *P. simplex*, and that an additional species, *P. ejectus* (SMITH, 1858) was also able to reduce CBB infestation in the laboratory (GONTHIER & al. 2015).

Some of the most compelling studies on ants and CBB have used exclosure techniques in the field to evaluate ants' potential to lower infestation on coffee plants. One of the earliest mentions of ants predating CBB is found in a nearly 100-year-old field report from Indonesia (LEEFMANS 1923). The author describes an experiment where *Dolichoderus bituberculatus* (SMITH, 1860) (now *D. thoracicus* (SMITH, 1860)) ants were attracted to coffee bushes by offering "nest opportunities", and the level of CBB infestation in fruits was monitored. This was compared to exclosure bushes that prevented ant foraging with a sticky barrier. After several months, infestation levels of CBB were nearly 10% lower in plants with ants compared to plants without ants (LEEFMANS 1923). More recently, GONTHIER & al. (2013) conducted an exclosure study in Mexico where outbreaks of CBB were simulated in the presence / absence of ants on coffee branches and infestation was measured after a 24 h period. The experiments were conducted on bushes dominated by different species of ants that were common on the farm. Pooling the species together, ants reduced CBB infestation by roughly 50% and six (*Azteca sericeasur*, *Pheidole synanthropica*, *Pseudomyrmex ejectus*, *P. simplex*, *Wasmannia auropunctata* (ROGER, 1863), and *Tapinoma* sp.) out of the eight ant species tested significantly reduced infestation (GONTHIER & al. 2013). A similar study used the same technique to measure the efficiency of infestation reduction by *A. sericeasur* under different densities of CBB (MORRIS & al. 2015). Here, ants consistently reduced CBB infestation on branches by about 70% to 80%, even at high borer densities of 80 individuals / branch (MORRIS & al. 2015). This may indicate that some species of ants could buffer future outbreaks when other conditions lead to increased CBB densities on coffee plants. Contrary to these studies, one long-term exclosure study (8 months) found no effect of general ant removal from coffee plants on CBB infestation (PHILPOTT & VANDERMEER 2008d).

Removal of CBB from inside berries on coffee plants: Another means for ants to contribute to CBB control and potentially reduce future damage in coffee farms is by predating borers while they are inside of coffee berries on plants (Fig. 1b). This may be crucial for effective CBB population suppression because borers spend most of their lives inside of berries where they are protected from chemical applications and larger predators. Additionally, infested berries that are missed and left on plants during harvest provide a refuge for CBB populations between coffee production seasons (BAKER & BARRERA 1993). Some literature suggests that smaller ants that forage on coffee can enter CBB galleries in infested berries on plants and remove individuals. However, many of these studies offer only anecdotal reports without providing

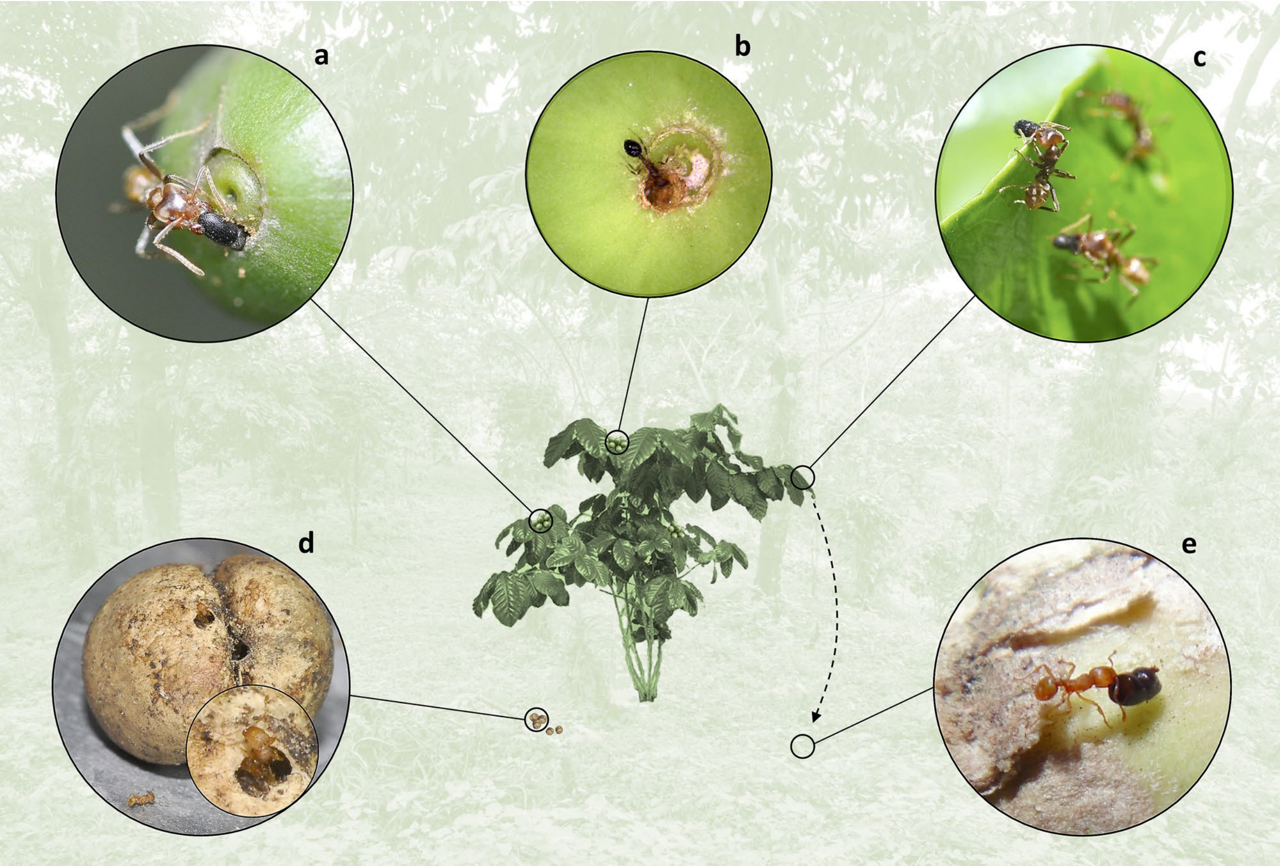

Fig. 1: Ant-coffee berry borer interactions. Because of the diversity of ant communities and the spatial complexity of coffee agroecosystems, ants can attack coffee berry borer (CBB) through a variety of mechanisms. (a) Ants attack colonizing CBB and reduce infestation. While CBB bore into coffee berries, a process which can take several hours, they are vulnerable to attack from ants that forage on coffee plants. Here, an *Azteca sericeasur* worker removes an adult CBB from a fruit that it has just begun to bore, preventing more serious damage to the berry. (b) Ants enter bored fruits on plants to predate CBB. Ant species that are small enough to move through CBB galleries can predate borers inside the fruits. Here, a *Solenopsis picea* worker explores an abandoned CBB gallery. (c) Non-consumptive effects of ants on CBB. Ants that tend hemipterans on coffee plants, like the *A. sericeasur* shown here, sometimes attack and remove CBB from coffee without consuming it – reducing infestation and making CBB vulnerable to predation on the ground (shown by dashed arrow). (d) Small ground foraging ants remove CBB from fallen fruits. Smaller ant species that forage on the ground, like this *Wasmannia auropunctata* worker, may enter galleries in fallen fruits and remove CBB adults and brood. (e) Ants attack free-roaming CBB on the ground. As CBB disperse, or are thrown from coffee plants by other ants, they are vulnerable to attack on the ground. Here, a *W. auropunctata* worker carries a free-roaming CBB adult back to the ant nest. Photographs: (a-d) Jonathan R. Morris, (e) Ivette Perfecto.

quantitative evidence on the potential of this behavior to reduce CBB densities on plants (Fonseca & Araujo 1939, Benassi 1995, Bustillo & al. 2002, Armbrecht & Perfecto 2003, Infante & al. 2003, Vázquez Moreno & al. 2006, Vázquez Moreno & al. 2009). For example, in Brazil, two studies report that the small ant *Crematogaster curvispinosa* Mayr, 1862 is frequently found in CBB galleries in fruits, but it is not clear if the ants aggressively predate CBB or are just opportunistically using the bored fruits as nesting space (Fonseca & Araujo 1939, Benassi 1995). A recent laboratory experiment tested the potential for two arboreal ant species to enter CBB galleries and to predate larvae and pupae of CBB (Morris & Perfecto 2016). Both *Wasmannia auropunctata* and *Solenopsis picea* Emery, 1896 significantly removed immature CBB that had been extracted from fruits, but only *W. auropunctata* readily entered CBB galleries in the experiment (Morris & Perfecto 2016). Another laboratory study, from Colombia, exposed *Crematogaster* sp. ants to immature CBB extracted from fruits and reported that this ant efficiently removed them (Vera-Montoya & al. 2007). They also collected green coffee fruits from farms and found *Crematogaster* ants and several other ant genera inside abandoned CBB galleries – indicating that these species may be able to enter fruits to predate CBB on plants (Vera-Montoya & al. 2007). Despite this evidence, it is still not known if ants efficiently predate immature CBB inside berries on plants in the field.

Only a few studies have experimentally tested the ability of ants to remove adult CBB from berries on plants. In Colombia, Gallego Ropero & Armbrecht (2005) used mesh bags of different hole sizes to manipulate ant access to coffee fruits. The bags were filled with treated parchment coffee (dried seeds with pulp removed) that was preexposed to adult CBB. Paired control and exclosure bags (ants / no ants) were placed on coffee plants in the field and the ant community on these plants was sampled. After five days, the berries were dissected and the number of fruits with adult CBB remaining inside was counted. Control bags had significantly lower CBB present in galleries, indicating the ant community removed a significant amount of adult CBB from within the coffee seeds (GALLEGO ROPERO & ARMBRECHT 2005). Additionally, several ant species were found inside CBB galleries, but one dominant species, *Solenopsis picea*, was found in 58% of dissected fruits. This experiment was also performed in the laboratory with coffee plants that were exposed to colonies of either *S. picea* or *Tetramorium simillimum* (SMITH, 1851) to isolate the predatory effects of individual ant species. In the lab, *S. picea* significantly reduced the number of adult CBB in bored parchment fruits by roughly 50%, but *T. simillimum* did not, despite being found inside CBB galleries in the field in 7% of cases (GALLEGO ROPERO & ARMBRECHT 2005). It appears that some species of ants may indeed be important predators of CBB inside fruits, but that all ant species that enter berries do not necessarily remove CBB adults, and may only enter after galleries are abandoned. This suggests that in addition to observation of ant behavior, quantitative studies are necessary to fully gage the predation potential of ants on CBB inside berries. Genetic analysis of gut contents, as has been performed with other CBB predators (JARAMILLO & al. 2010), may further illuminate the consumption of CBB by ants inside berries. However, this technique may be more difficult in ants if workers typically consume only liquid food, and instead feed prey solids to larvae (WENT & al. 1972).

In Mexico, LARSEN & PHILPOTT (2010) investigated the role of twig-nesting ants in removing CBB adults from berries on coffee plants. The authors used similar methods to GALLEGO ROPERO & ARMBRECHT (2005), but instead used infested green coffee berries collected from the field and left berries on plants for 15 days. After dissecting berries, the authors found that in a plot of low agricultural management intensity (high density and diversity of shade trees) borer levels were reduced nearly 50% by the ant community, but in other more intensified farms there was not a significant reduction (LARSEN & PHILPOTT 2010). In the laboratory, LARSEN & PHILPOTT (2010) exposed colonies of three twig-nesting ant species, *Pseudomyrmex simplex*, *P. ejectus*, and *Pseudomyrmex* sp., to free-roaming adult CBB and CBB in infested green berries. After 24 h, all three ant species significantly removed free-roaming adult borers and reduced the number of adult borers found in berries by 31% to 46% compared to controls (LARSEN & PHILPOTT 2010). Ants were also observed carrying CBB individuals back to their nest and CBB parts were recovered inside nests, suggesting predation.

Ground predation of CBB: In addition to CBB suppression on coffee plants, ant predation of CBB on the ground is also important for biocontrol. Infested fruits fall to the ground as they senesce, or as they are dropped from plants during harvest. These berries serve as an important source for the population of borers between coffee growing seasons when new fruits are not available for colonization (BAKER & BARRERA 1993, DAMON 2000, ARISTIZÁBAL & al. 2016). Studies have tested ground-foraging ant predation on CBB in berries (Fig. 1d) and on free-roaming CBB (Fig. 1e).

Ant predation on free-roaming CBB on the ground was tested by ARMBRECHT & GALLEGO (2007) using traps to manipulate CBB and ants. Glass traps maintained CBB adults inside, and either allowed ants to pass in and out freely, or prevented ant entry with a fluoropolymer resin. Control and treatment traps (ants / no ants) were placed on the ground in coffee farms and left for five days to measure ant removal rates of CBB. Upon collection, the authors recorded 18 different species of ants across all traps, with at least one species present in the majority of traps, and found that the ant community significantly removed or killed nearly 50% of CBB (ARMBRECHT & GALLEGO 2007). Using the same technique in the laboratory, the authors exposed colonies of three common ground-foraging ant species (*Paratrechina* cf. *steinheili* (FOREL, 1893), *Tetramorium simillimum*, *Solenopsis* cf. *picea*) to free-roaming adult CBB. All three species significantly removed or killed CBB in traps by 75% to ~100% after five days (ARMBRECHT & GALLEGO 2007).

In a recent study conducted in Thailand, authors collected seven species of ground-foraging ants from coffee farms and exposed ants to adult CBB in the laboratory (ONISHI & al. 2017). They found that *Anoplolepis gracilipes* (SMITH, 1857), *Camponotus nicobarensis* MAYR, 1865, *Crematogaster* sp., *Dolichoderus* sp., *Tapinoma* sp., *Technomyrmex modiglianii* EMERY, 1900, and *Technomyrmex yamanei* BOLTON, 2007, attacked CBB individuals and all but, *A. gracilipes* carried the borers with their mandibles (ONISHI & al. 2017). This is one of the few ant-CBB studies conducted outside of Latin America and shows promise that ant conservation biocontrol measures in coffee may be effective over a broader geographic range.

While predation of free-roaming CBB adults on the ground is important for control, ground-foraging ants are more likely to encounter CBB embedded in berries, since the borers spend most of their life cycle there. In Costa Rica, VARÓN & al. (2004) removed immature and adult CBB from infested berries and placed them inside containers which were connected to ant colonies of five different ground-foraging species kept in the laboratory. Four of five species tested (*Solenopsis geminata* (FABRICIUS, 1804), *Pheidole radoszkowskii* MAYR, 1884, *Crematogaster crinosa* MAYR, 1862, and *C. torosa* MAYR, 1870) significantly removed egg and larval stages of the borers, but only *S. geminata* and *P. radoszkowskii*, took a significant number of adult CBB (VARÓN & al. 2004). Interestingly, *C. curvispinosa*, a species which has been suggested to remove CBB from berries in Brazil (FONSECA & ARAUJO 1939, BENASSI 1995), failed to remove a significant number of any CBB life stage. VARÓN & al. (2004) then tested the ability of the ground ants to remove CBB from galleries in infested berries in the field. Infested parchment berries were placed in exclosure and control petri dishes, to manipulate ant presence, which were placed on the ground around colonies of *S. geminata*, *P. radoszkowskii*, and *C. torosa*. After 48 hours, berries were collected and dissected to examine the number of CBB remaining inside. Despite demonstrating that ants can efficiently predate CBB in the laboratory the authors failed to find an effect of the ants on any life stage of CBB in berries in the field, perhaps because the ant species tested were too large to fit into CBB galleries in berries (VARÓN & al. 2004).

In another field study in Costa Rica, TRIBLE & CARROLL (2014) investigated the ability of the general ground ant community to remove CBB from berries. The authors placed clusters of infested green berries in plots on the ground and dissected batches of berries to measure the number of CBB in fruits before and after exposure to ants. They also removed the competitively dominant ant, *Solenopsis geminata* from some plots and compared ant community removal rates of CBB between plots with and without *S. geminata* after 72 h. In all plots where *S. geminata* had been removed, rates of CBB adult removal by ants in green berries were significantly higher (~ 23%) than in plots with *S. geminata* (~ 7%) (Trible & Carroll 2014). This study provides evidence that smaller ant species may contribute to CBB population suppression on the ground by entering berries and removing adults. However, large, dominant ant species may interfere with CBB suppression in ground fruits if they competitively exclude smaller ants which more readily enter galleries to predate CBB.

Post-harvest control of CBB may also occur with ground-foraging ants. In Colombia, Vélez & al. (2006) found that ground ant communities removed 82% to 92% of CBB that exit coffee berries during the drying process in parabolic solar dryers, compared to ant-exclosure controls. Six ant species (*Solenopsis geminata*, *Pheidole* sp., *Mycocepurus smithii* (Forel, 1893), *Dorymyrmex* sp., *Ectatomma ruidum* (Roger, 1860), and *Odontomachus erythrocephalus* Emery, 1890) were observed foraging inside dryers during the study. Their results indicate that ants have the potential to reduce further CBB damage to healthy berries by suppressing borer populations that escape during coffee processing (Vélez & al. 2006). More efforts should be allocated to studying the potential of ants in post-harvest biocontrol, considering that most coffee produced by smallholder farms relies on traditional solar drying techniques that could allow ant access (Vélez & al. 2006).

Biodiversity, ecological complexity, and CBB biocontrol function

Considering the abundance of individual case studies, there is compelling evidence that a number of ant species are antagonists of CBB and can suppress CBB infestation on farms. Despite these examples, we warn against a reductionist, quick-fix approach, which might promote the transfer of individual ant species to coffee farms. Aggressive ants, when introduced outside of their native range, can become problematic invasive species, leading to costly disservices and negative impacts on native biodiversity (Del Toro & al. 2012). Alternatively, conservation biocontrol aims to conserve communities of natural enemies, not over-relying on individual species, which not only better conserves diversity, but may also provide more robust biocontrol (Straub & al. 2008, Letourneau & al. 2009, Crowder & Jabbour 2014). In coffee agroecosystems, ant communities are diverse and embedded in complex food webs and interaction networks (Philpott & Armbrecht 2006, Vandermeer & al. 2010). Both biodiversity and ecological complexity work in concert to determine the overall function of ant-mediated biological control (Wielgoss & al. 2014), and thus, the provision of this service in coffee agroecosystems. To comprehensively evaluate the potential of this ecosystem service and to answer practical questions about impacts on yield and coffee farm management, we examine the relationship between ant diversity, interaction complexity, and ant-CBB biocontrol function.

Ant diversity: Ant communities in coffee farms are diverse, in some cases similar in species richness to nearby forest communities (Perfecto & Snelling 1995, Perfecto & Vandermeer 2002, Armbrecht & Perfecto 2003, Armbrecht & al. 2005). Diversity in ant communities (both richness and relative abundance) can have positive, negative, or neutral effects on CBB biocontrol. De la Mora & al. (2015) showed that ant diversity on coffee plants positively correlates with CBB sentinel prey removal and Vazquez & al. (2009) found a negative correlation between arboreal ant richness and CBB infestation – but whether there is a general effect of ant diversity on CBB biocontrol is still unknown. Diversity effects of consumers can occur through a variety of direct and indirect mechanisms, and therefore may be more difficult to demonstrate experimentally, as has been shown with producers (Duffy 2002, Duffy & al. 2007). Here, we review some of these potential mechanisms using the few studies on ant-CBB biocontrol that have addressed them.

Individual aggressive predatory ant species and species with efficient recruitment rates will likely have stronger effects on CBB than other ant species. However, increasing ant diversity may increase the likelihood that an aggressive species is present by chance through the sampling effect (Huston 1997, Loreau & Hector 2001). Also, while individual dominant ant species may have a greater impact on CBB biocontrol than others, because ant communities typically assemble in mosaic patchworks (Adams 2016, Perfecto & Vandermeer 2013) the collective community of ants will determine the overall level of control. In farms with high ant diversity, species that can efficiently suppress CBB may not commonly occupy coffee bushes. For example, the keystone ant *A. sericeasur*, which suppresses CBB infestation on coffee plants (Gonthier & al. 2013, Morris & al. 2015), is typically only found on fewer than 10% of coffee plants in farms where it has been studied (Vandermeer & al. 2010, Jiménez-Soto & al. 2013).

Increasing ant species richness on farms can enhance overall biocontrol if ant species complement each other in communities. Complementarity can occur through two general non-exclusive mechanisms, niche or resource partitioning (additive effects) and facilitation (non-additive effects), and both require functional diversity amongst species (Crowder & Jabbour 2014). With CBB predation and biocontrol, niche or resource partitioning in ants may occur through a variety of mechanisms. Ants on coffee farms vary in their foraging behavior and recruitment rates to prey (Philpott & al. 2008c) and specifically in how they respond to CBB on coffee plants (Jiménez-Soto & al. 2013). Ant species also are likely to show temporal and spatial complementarity (Albrecht & Gotelli 2001). Different species of ants forage at different times of day, with some peaking in activity at night, while others are mainly active during the day (Albrecht & Gotelli 2001). This may allow multiple species to attack CBB in the same space on farms while minimizing interference between ant species. The same effect may occur on seasonal time scales if colonies of different ant species require resources at different times through the year. There is also potential for ant species complementarity through spatial partitioning. Because different species of ants typically specialize in foraging either on the ground or arboreally (Perfecto & Vandermeer 2013), presence of species from each group will enhance the overall consumption of CBB. Facilitation between ant species may occur through this spatial effect as well, if ants in the coffee plant spatial layers make borers more available to ants on the ground by knocking them off plants (Jiménez-Soto & al. 2013, Morris & al. 2015).

In contrast to the positive effects of increasing ant richness, increased diversity in ant communities on coffee farms may have neutral effects if ants are functionally redundant to each other. Studies which test for diversity effects within functional groups of ants may be less likely to find positive effects of diversity. However, the insurance hypothesis of biodiversity (Yachi & Loreau 1999) suggests functional redundancy may result in more robust CBB suppression, if ant species respond differentially to ecological change. Philpott

& al. (2012) demonstrated this possibility in a laboratory study with three species of ants. They showed that CBB infestation reduction by ants in tent cages was equivalent in one vs. three species treatments, suggesting ant functional redundancy. However, when phorid parasitoids were introduced into these cages the activity of the phorid's host, *Azteca sericeasur*, was reduced and multispecies groupings were necessary to rescue CBB infestation suppression (Philpott & al. 2012). The authors suggest this serves as an example of the insurance hypothesis – while ant diversity may not be important in some circumstances, it can become critical for successful biocontrol as conditions change.

In other circumstances, ant biodiversity may detract from overall CBB control if ant species interact in antagonistic ways through competition or intraguild predation. Interference may be likely within functional groups or foraging guilds of ants, as ant species often maintain spatial territories and engage in competitive networks (Adams 2016, Perfecto & Vandermeer 2013). For example, dominant ant species that outcompete smaller ants may detract from the removal of CBB in coffee fruits on the ground, reducing CBB suppression. This was demonstrated with *Solenopsis geminata*, a large competitively dominant ant, which excludes smaller ants from its territory, indirectly reducing within berry CBB removal rates (Trible & Carroll 2014). However, *S. geminata* also predates free-roaming CBB adults (Varón & al. 2004, Vélez & al. 2006), so the net effect of its presence in ground ant communities may still be positive. Negative competitive effects also occur on coffee plants with the aggressive arboreal ant, *Azteca sericeasur*, which can exclude other smaller ant species that prey on CBB inside of berries on plants (Philpott 2010), possibly resulting in increased damage once CBB are established inside berries on coffee plants with *A. sericeasur* (Jiménez-Soto & al. 2013). However, since *A. sericeasur* significantly reduces the overall level of CBB infestation (Gonthier & al. 2013, Jiménez-Soto & al. 2013), this ant species still likely has a beneficial net impact. While antagonistic interactions between ant species likely do reduce the efficiency of biocontrol in some cases, a growing body of theoretical and empirical literature on interaction complexity suggests that antagonisms between species can sometimes stabilize interaction dynamics and may counter-intuitively enhance community-level biocontrol. This potential has been explored in terms of intraguild predation (Ong & Vandermeer 2014, 2015) and intransitive competition (Vandermeer 2011). However, this has yet to be demonstrated with ants in coffee.

Despite the examples discussed above, our mechanistic understanding of the relationship between ant diversity and biocontrol function is still limited. Many of the potential processes we outlined have yet to be tested and there are still many unexplored mechanisms we have surely overlooked.

Interaction complexity: Beyond ant diversity per se, other biotic components of coffee agroecosystems may be important for determining overall biocontrol function. Interactions between ants and other species in food webs (Duffy & al. 2007) and complex interaction networks (Eubanks & Finke 2014) on coffee farms (Vandermeer & al. 2010, Perfecto & al. 2014) will affect the overall efficiency of ants to control CBB. These interactions may cascade in these systems to enhance or detract from ant-mediated biocontrol.

Because most ants are generalist consumers, ant species that predate CBB likely prey on a host of other organisms (Way & Khoo 1992, Symondson & al. 2002). The effect of generalist predators vs. specialists has been discussed in the biocontrol literature, where theory suggests that generalists may not be as efficient as specialists in controlling pests if they are consuming alternative prey (Symondson & al. 2002). However, generalists may persist with more stability if their populations are supported by a variety of resources (Symondson & al. 2002). For example, predatory ants that consume large numbers of CBB may switch to other prey resources when CBB populations are low. One study tested the impact of pest diversity on pest control by ants in single species and diverse assemblages of ants (3 spp.) (Gonthier & al. 2015). In laboratory experiments the authors found that the ability of single ant species to reduce herbivory on coffee was reduced when ants were presented with multiple prey species (including CBB) as opposed to single prey species, suggesting a negative effect of prey diversity. However, this effect was negated in diverse ant treatments (with 3 spp.), suggesting that predator and prey diversity may interact to enhance or stabilize coffee pest control. While the mechanism for this result is unknown, and may be driven by diversity effects among predators, such as partitioning or facilitation, the authors emphasize the general importance of considering diversity impacts on biocontrol function from multiple trophic levels in complex coffee agroecosystems (Gonthier & al. 2015).

Multi-trophic impacts on ant-CBB biocontrol should also be considered in regards to natural enemies of ants. Diverse coffee farms can support populations of ant parasitoids and predators, which may detract from CBB biocontrol. When phorid parasitoids attack *Azteca sericeasur*, the ants respond by lowering their activity level, which reduces their ability to attack borers. Two studies demonstrated this important trait-mediated indirect interaction (TMII) (Pardee & Philpott 2011, Philpott & al. 2012), but Philpott & al. (2012) found that the presence of additional ant species can rescue CBB infestation suppression when *A. sericeasur* is compromised by phorids.

CBB biocontrol may also be impacted by interactions between ants and other intraguild predators that consume CBB, such as with birds, anoles, and spiders (Henaut & al. 2001, Karp & al. 2013, Monagan & al. 2017). In these cases, intraguild predation or interference may result in reduced biocontrol efficiency (Finke & Denno 2004, Vance-Chalcraft & al. 2007). This likely occurs when aggressive ants occupy coffee bushes, preventing other predators from foraging, or when birds (Karp & Daily 2014) and anoles (Monagan & al. 2017) consume ants, reducing the ants' predatory impact on CBB. In other cases, ants may indirectly benefit other predators as they attack and throw CBB from plants, making them more available to predators on the ground (Jiménez-Soto & al. 2013, Morris & al. 2015). This has been demonstrated in other systems, where the spatial partitioning of natural enemies in plants drives predator facilitation (Losey & Denno 1998). Ant presence is also linked to increased densities of certain web-building spiders in coffee (Marín & al. 2015), which could increase spider predation of dispersing CBB and CBB thrown by ants. Depending on the overall strength and direction of these interactions, intraguild diversity across these groups may also help to stabilize CBB control and dampen the effects of environmental variability, as different predatory groups compensate for one another during varying ecological changes (Crowder & Jabbour 2014). This is an area of research that needs to be further investigated for CBB biocontrol.

Ant-hemipteran interactions: One of the most important examples of trophic complexity in ant control of CBB is the interaction of ants and hemipteran insects – a widespread relationship and a major driver of ant function in tropical ecosystems (Styrsky & Eubanks 2007). In ant-hemipteran interactions, ants are attracted to plants by carbohydrate resources made accessible by phloem-sucking hemipteran insects (aphids, tree hoppers, scales, etc.) (Styrsky & Eubanks 2007). Generally, ants consume the sugar rich excrement from hemipterans, in the form of "honeydew", and in turn "tend" these hemipterans, protecting them from natural enemies. Ants that tend hemipterans often aggressively defend them from disturbance, including other herbivores that may damage the plant (Styrsky & Eubanks 2007). The net impact of this interaction on the host plant can be negative, if ants increase hemipterans to pest levels that damage the host plant more than the other herbivores that are attacked by ants, or if hemipteran insects spread diseases that damage the host plant. For these reasons, ants are sometimes considered indirect pests when they are found tending hemipterans in farms (Philpott & Armbrecht 2006). However, when ants aggressively defend plants from more damaging herbivores, such as CBB, they can offer a net benefit to the plant, resulting in an indirect mutualism. The ant-hemipteran interaction thus represents a trade-off of resources for the host plant (energy for defense), and whether the net result of these interactions is negative or positive for plants is context-dependent. Most often, hemipteran-tending ants result in a net benefit to plants, especially in tropical and perennial systems like coffee (Styrsky & Eubanks 2007, Rosumek & al. 2009, Trager & al. 2010) and in many cases ant-hemipteran interactions may be essential for successful ant-mediated biocontrol (Way & Khoo 1992).

On coffee, ant-hemipteran interactions occur frequently, especially between ants and the green coffee scale, *Coccus viridis* (Fig. 2) (Vandermeer & al. 2010, Perfecto & al. 2014). On other plants, tending of *C. viridis* by ants can result in high scale densities leading to leaf abscission and death due to the growth of sooty mold on the plant surface (Bach 1991). However, when ants aggressively defend scales on coffee, they can significantly lower CBB infestation by attacking adult CBB, an example of the classic trade-off of ant-plant interactions. Interestingly, some aggressive ant species that receive most of their nutrients from scales may not consume CBB, but instead attack them and throw them from plants or cause them to fall (Jiménez-Soto & al. 2013) (Fig. 1c). While non-consumptive effects of ants on CBB can reduce infestation on plants the ants occupy, borers that are removed from plants may not be killed and could potentially infest other coffee plants nearby. However, adult CBB removed by ants on plants often fall to the ground (Jiménez-Soto & al. 2013), making them vulnerable to consumption by other predators, as described above. Additionally, these non-consumptive effects may allow ants to efficiently suppress CBB infestation, even under high densities of CBB, if ants avoid satiation by not consuming prey (Morris & al. 2015).

Further complexities have been revealed in this relationship with the keystone ant species *Azteca sericeasur*, which is a key player in a complex interaction network in Mexican coffee agroecosystems (Vandermeer & al. 2010, Perfecto & al. 2014). The interaction between *A. sericeasur* and *Coccus viridis* on coffee may be self-limited by the numerical responses of natural enemies to the ant-scale

Fig. 2: Ant-hemipteran interactions on coffee. Many species of arboreal ants forage on coffee and tend hemipteran insects in exchange for honeydew. Ants that tend hemipterans often aggressively defend them and indirectly protect their host plant from other herbivores, such as the coffee berry borer (CBB). (a) Here, *Azteca sericeasur* workers tend the green coffee scale insect, *Coccus viridis*, while one ant attacks a CBB adult on a coffee leaf. (b) *Wasmannia auropunctata* workers, known predators of CBB, tend *C. viridis* on a coffee leaf. Photographs: Jonathan R. Morris.

complex. One of these, a generalist fungal entomopathogen of the scale, *Lecanicillium lecanii*, also attacks coffee leaf rust, another devastating pest of coffee (Perfecto & al. 2014). Furthermore, the spatial patchiness of the *A. sericeasur*-*C. viridis* interaction helps maintain a coccinellid predator of the scale, whose larval stage benefits from indirect protection by *A. sericeasur* on coffee plants (Vandermeer & al. 2010). This case study calls for more careful consideration of ant-hemipteran interactions in the context of complex interaction networks.

Promoting conservation biocontrol: managing ants and CBB in coffee agroecosystems

Considering the complexities outlined above, it is clear that conservation biocontrol in coffee requires a holistic approach. The central tenant of this approach is that the conservation of habitat in and around coffee farms will support natural enemy communities and the ecological networks in which they are embedded, thereby indirectly supporting biological pest control on farms. This may also promote biodiversity more generally, enhancing the conservation value of farms. Ultimately, this approach has the potential to result in multi-win scenarios, both through conserving biodiversity, promoting biocontrol services, and enhancing yields (Iverson & al. 2014). Generally, biodiversity in agricultural systems is affected by two scales of ecological conditions – local factors and landscape factors (Gonthier & al. 2014). Local factors include the effects of farm management, such as agrochemical inputs and vegetation complexity, and landscape factors include the composition of the agricultural matrix, such as the amount of forest patches surrounding farms. It is also clear that these factors interact, where the impacts of landscape factors may be mediated by local conditions on farms (Tscharntke & al. 2005). In a meta-analysis, Gonthier & al. (2014) show that different taxonomic groups are impacted differentially by these factors, but that arthropod diversity and abundance is impacted both by local and landscape factors, requiring a multiscale approach to conservation. Here we review relevant literature on the impact of local and landscape factors on ant diversity and CBB biocontrol services. We also consider some of the potential secondary impacts on CBB populations.

Coffee farm management (local factors): There is a rich literature on the impacts of coffee farm management and farm intensification on biodiversity (Perfecto & al. 1996, Moguel & Toledo 1999, Philpott & al. 2008a, Tscharntke & al. 2011, Jha & al. 2014). Typically, coffee intensification alters vegetation complexity by modifying or reducing shade trees, shade cover, tree density, average tree height, canopy layers, epiphyte density and diversity, and herbaceous plant diversity and ground cover (Moguel & Toledo 1999). These modifications reduce habitat complexity and limit resources, such as decomposing wood, twigs, and leaf litter (Perfecto & al. 1996). Farm intensification also often results in increased coffee plant density and increased use of agrochemicals, including fertilizer and pesticides (Moguel & Toledo 1999). Intensification in coffee systems usually occurs along a gradient, where farms fall into various categories based on their general level of intensification, and specific local factors vary in degree depending on the farm type (Moguel & Toledo 1999). Collectively, changes in local ecosystem factors can have drastic impacts on on-farm biodiversity.

Most research investigating the local drivers of ant biodiversity in coffee agroecosystems examines correlations between different ant communities (typically ground and arboreal) and vegetation complexity, which we refer to generally as "intensification". In ground-foraging ant communities, most studies have found negative impacts of intensification on diversity. Many of these have shown reduced ground ant species richness when comparing low intensive systems to high intensive systems (Perfecto & Snelling 1995, Perfecto & Vandermeer 1996, Perfecto & Vandermeer 2002, Armbrecht & Perfecto 2003, Perfecto & al. 2003, Armbrecht & al. 2004, Armbrecht & al. 2005), although a few studies find no impacts of intensification on ground ant species richness (De la Mora & Philpott 2010, De la Mora & al. 2013, Murnen & al. 2013). Ground ant abundance also generally declines with intensification and loss of vegetation complexity (Perfecto & Snelling 1995, Perfecto & Vandermeer 1996, De la Mora & al. 2013, Murnen & al. 2013).

With arboreal ant communities, studies are sparser and general trends are less clear. Some studies suggest that arboreal and coffee-foraging ant richness is negatively impacted by intensification (Perfecto & al. 1997, Philpott & Foster 2005, Philpott & al. 2006a, Jiménez-Soto & Philpott 2015), while others have found no differences between high and low intensity farms (Perfecto & Snelling 1995, Armbrecht & al. 2005, Larsen & Philpott 2010, De la Mora & al. 2013). Most studies have found no effects of intensification on arboreal ant abundance (Perfecto & Snelling 1995, Philpott & al. 2006a, De la Mora & al. 2013, Jiménez-Soto & Philpott 2015), with only a few showing reductions with intensification (Perfecto & al. 1997, Philpott & Foster 2005), and one contrasting study which found increased ant abundance with lower shade levels (Karungi & al. 2015). It is possible that the negative impacts of vegetation complexity loss on arboreal ant communities are not as pronounced as with ground ants because they are counteracted by increases in coffee plant density associated with intensification, which provide resources for some arboreal species. However, in the most extreme cases, where all shade trees are removed, many arboreal ant species will likely be lost (Perfecto & al. 1997).

Only a few studies have tested for local-level mechanisms associated with intensification that impact coffee ant diversity. In Costa Rica, Perfecto & Vandermeer (1996) investigated the impact of changes in microclimate by manipulating shade, light, and leaf litter cover. They found that reduced leaf litter and increased light on the forest floor allowed the competitively dominant *Solenopsis geminata* to thrive, which indirectly reduced diversity of other ground-foraging ants (Perfecto & Vandermeer 1996). Ant biodiversity may also be lost if reductions in vegetation complexity limit nesting resources for ants. This has been supported in particular groups of ground-foraging ants, such as twig nesters (Armbrecht & al. 2004), but not with others, such as wood nesting ants (Murnen & al. 2013). In experiments that manipulate nest site availability on trees and coffee plants, adding artificial bamboo nests can promote ant diversity, suggesting that some arboreal ants may be nest site limited as well (Philpott & Foster 2005, Jiménez-Soto & Philpott 2015). Thus, pruning and removal of dead branches on shade trees and coffee plants, which often occurs with farm intensification, may reduce nesting resources for some arboreal ants.

Many other possible drivers of ant diversity of coffee farms remain to be tested. In arboreal communities, changes in ant biodiversity may be driven by the removal of epiphytes and moss from shade trees and coffee trunks under which many coffee foraging species can nest (Perfecto & al. 1996, Morris & Perfecto 2016). On farms that use herbicides or aggressively cut "weedy" vegetation, ant diversity may decline to due adverse changes in resources or microclimate conditions (Nestel & Dickschen 1990). Beyond vegetation complexity and shade, other intensification related factors may impact ant diversity. Heavy use of agrochemicals, especially insecticides, may directly impact ant colonies or reduce prey abundance which could result in diversity loss on intensive farms (Perfecto 1990). However, in two recent studies that correlated coffee agrochemical use to ant communities, no significant effects were found (De la Mora & al. 2013, 2015), although it is not clear what proportion of these chemicals were insecticides.

More mechanistic research on how local coffee farm factors impact ant biodiversity is needed to pinpoint the most important components of managing for ants and CBB conservation biocontrol. This may also open the door to possibilities for augmentation of ant-mediated CBB control. For example, use of artificial bamboo nests on coffee plants may provide additional nesting resources for ant communities (Philpott & Foster 2005, Jiménez-Soto & Philpott 2015) or the use of bamboo or rope to better connect plants may allow arboreal ants to more efficiently encounter prey (Huang & Pei 1987, Offenberg 2015).

Beyond the impacts of local management factors on ant diversity, some research has addressed the impact of local-scale farm factors on the efficiency of CBB suppression by ants. Farms with more vegetation complexity and shade have higher rates of CBB removal by ants both on the ground (Armbrecht & Gallego 2007), and in coffee plants (Gallego Ropero & Armbrecht 2005, Larsen & Philpott 2010). Because these studies did not isolate these effects with specific species of ants, the findings may be an indirect result of a general increase of ant diversity in low intensity farms. However, Larsen & Philpott (2010) showed that while diversity of twig-nesting ants on coffee plants did not change with farm intensification, CBB removal rates by ants in berries were highest in low intensity farms, indicating an emergent property of intensification on borer removal rates by ants. Conversely, one study found few significant impacts of local factors on ant removal rates of CBB sentinel prey, but instead found that ant diversity and abundance was a more significant driver of removal efficiency (De la Mora & al. 2015).

CBB populations may also be impacted by local farm management factors. Conventional recommendations on CBB management have typically asserted that shade and vegetation complexity in low intensity farms may enhance CBB populations (see citations in Vega & al. 2015). However, recent quantitative examinations of this claim have been mixed. Studies have found no effect of moderate shade levels on CBB infestation levels (Soto-Pinto & al. 2002, Teodoro & al. 2009), higher infestation with shade (Bosselmann & al. 2009, Larsen & Philpott 2010, Mariño & al. 2016), and reduced infestation with shade (Jaramillo & al. 2013, Jonsson & al. 2014). Mariño & al. (2016) found that, while shaded farms had higher levels of infestation, sun farms had more CBB individuals and a higher proportion of females (boring individuals) per fruit. Most of these studies however, rely on correlations, which limits inference on the effect of farm vegetation complexity on CBB populations. Indeed, other management factors associated with high vs. low shade farms may be more responsible for driving CBB densities than shade. Larsen & Philpott (2010), which found higher levels of CBB infestation with more shade, also found higher levels of coffee seedlings around plants on less intensive farms, indicating less thorough removal of berries during harvests. Other factors linked to farm intensification, such as the use of pesticides, may be driving some of the mixed trends found in the literature. Thus, it is not yet clear whether increased shade and vegetation complexity has a significant direct effect on CBB densities.

The agricultural matrix (landscape factors): Less is known about landscape impacts on ant diversity or biocontrol in coffee farms, although the general literature on this subject is rich (Perfecto & al. 2009). Theory suggests a high quality agricultural matrix helps to preserve source populations, enhance dispersal, and maintain metapopulation dynamics that counteract local extinctions (Perfecto & Vandermeer 2008, Perfecto & al. 2009, Perfecto & Vandermeer 2010), all of which could promote natural enemies. Other general work has related landscape factors to biocontrol services specifically (Tscharntke & al. 2005, Bianchi & al. 2006), indicating that natural enemies and pest control may benefit from complex landscapes. In studies of ant diversity in coffee systems, research has focused on two general components of landscape – forest composition and distance to forest patches. Coffee sites with a high percent composition of surrounding forest can support higher levels of ant diversity (Perfecto & Vandermeer 2002, De la Mora & al. 2013). Increased distance to nearby forest patches also correlates with reduced ant diversity on farms (Armbrecht & Perfecto 2003, De la Mora & al. 2013, Karungi & al. 2015), however, this effect may interact with local management factors, where high levels of shade on farms can maintain ant diversity despite increasing distance from forest fragments (Perfecto & Vandermeer 2002, Armbrecht & Perfecto 2003). However, Karungi & al. (2015) found the opposite effect, where the negative relationship between ant abundance and distance from nearby forest was reduced on low shade farms.

Landscape factors may also affect CBB biocontrol through direct effects on CBB populations or by altering ant-CBB interactions. Coffee farms surrounded by larger amounts of forest cover can have lower CBB infestation rates (Avelino & al. 2012). High quality agricultural matrix with forest fragments interspersed between farms may impede CBB dispersal, by reducing coffee resources, and limit their populations (Avelino & al. 2012). In the one study that has examined landscape impacts on CBB control by ants, forest cover and distance to forest did not affect ant removal rates of dead CBB adults (De la Mora & al. 2015). While landscape level management of CBB biological control may be more difficult for individual coffee farmers to address, this may be a promising pest control strategy for coffee producing regions.

Assessing ant conservation biocontrol in coffee: additional benefits, disservices, and yield

Further assessing the impact of ant-CBB conservation biocontrol on overall coffee production requires consideration of some additional factors. There may be other general benefits or drawbacks of ants in coffee agroecosystems, as well as indirect positive and negative impacts, and trade-offs between ecosystem services, from agroecological measures taken to promote ant conservation biocontrol (Wielgoss & al. 2014). Consideration of these factors as well as the complexities presented above is necessary for a realistic assessment of this potential ecosystem service.

Additional benefits: Overall pest control in coffee may be enhanced by measures taken to promote ants. Generalist ants which consume or antagonize CBB have the potential to suppress other important coffee pests (Way & Khoo 1992, Symondson & al. 2002). This has been demonstrated with lepidopteran larvae (Vandermeer & al. 2002, Philpott & al. 2008c, Milligan & al. 2016), leafhoppers and leaf-chewing beetles (Gonthier & al. 2015), the coffee twig borer (*Xylosandrus compactus* (Eichhoff, 1875)) (Egonyu & al. 2015, Ogogol & al. 2017), and the coffee leaf miner

(*Leucoptera coffeella* (Guérin-Méneville, 1842)) (De la Mora & al. 2008). Other natural enemies may also benefit from ant conservation. Bird communities are bolstered by coffee shade trees and nearby forest patches, and can significantly reduce CBB infestation (Kellermann & al. 2008, Johnson & al. 2010, Karp & al. 2013) and other coffee herbivores (Perfecto & al. 2004, Sherry & al. 2016). There is evidence this also occurs with anoles (Borkhataria & al. 2012, Monagan & al. 2017) and spiders (Henaut & al. 2001, Ibarra-Núñez & al. 2001, Hajian-Forooshani & al. 2014) on CBB and other herbivores, and with bats on coffee leaf herbivores (Williams-Guillén & al. 2008).

Beyond pest control, ants may also benefit coffee production through interactions with pollinators. An exclosure study conducted in Mexico found that the interaction between ants and pollinators on coffee plants resulted in the highest levels of fruit set and fruit weight (Philpott & al. 2006b). Although the mechanism was not tested, it was hypothesized that ants may antagonize pollinators on coffee causing them to visit a higher number of flowers on different plants, which increases outcrossing and benefits fruit production.

Numerous additional benefits may come indirectly from local and landscape management measures taken to promote conservation biocontrol in coffee. Much has been written on the general benefits of shade and vegetation complexity in coffee and on the many potential ecosystem services promoted by low intensity farm management, which can increase the short-term and long-term productivity of farms (Perfecto & al. 1996, Tscharntke & al. 2011, Jha & al. 2014). These include services such as enhanced pollination and fruit set, weed suppression, reduced soil erosion, storm resilience, carbon sequestration, and the production of other agroforestry products (Jha & al. 2014).

Potential disservices: The main potential drawback of ant conservation in coffee is that hemipteran-tending by arboreal ants can harm plants when hemipterans increase to high densities. In the worst cases this could reduce the productivity of individual coffee plants. However, while scale insects can become pests at high densities, the coffee berry borer is considered a more significant pest of coffee since it directly attacks the fruit (Jaramillo & al. 2006). Furthermore, aggressive scale-tending ants may be limited in complex, low-intensity coffee systems by endogenous factors, such as ant parasitoids and scale entomopathogens, which have numerical responses to high densities of the ant-scale complex (Vandermeer & al. 2010, Perfecto & al. 2014).

Despite the benefits of ants, coffee farm workers typically have a negative view of ants. Ants on coffee plants and in the soil can attack workers during harvests (Philpott & Armbrecht 2006, Offenberg 2015). This is especially true of aggressive and sometimes invasive species such as the fire-ants *Solenopsis geminata* and *Wasmannia auropunctata.* Although these species may suppress CBB, their attacks on workers can make harvests more difficult and potentially increase labor costs. While this is a legitimate drawback, there are methods of sustainably managing aggressive ants, such as the use of lime or water on bushes to temporarily reduce their activity (Offenberg 2015).

The indirect potential drawbacks of ant conservation in coffee center on the impacts of maintaining shade on coffee yields. Generally, high levels of shade, such as are found in rustic coffee reduce coffee productivity (Perfecto & al. 2005); however, this negative impact may fade with moderate shade levels (Jha & al. 2014). Some studies have found that moderate shade levels (30% - 45%) on farms result in the highest levels of productivity, over intensive sun monoculture farms (Soto-Pinto & al. 2000). Despite this, comparative evaluation of shade impacts on productivity is difficult, and can be confounded by variability in other costly management factors, especially the input of agrochemicals, which may accompany intensification.

Yield: A major aim of this paper was to present the complexity of assessing a specific biocontrol service, especially in regard to questions about crop productivity and yield. While it is clear that ants predate CBB and can significantly reduce CBB infestation levels, the potential trade-offs of hemipteran-tending by arboreal ants may detract from the benefits of CBB biocontrol for coffee production. Unfortunately, few studies have assessed the overall impact of ant-mediated biocontrol on coffee yields. This contrasts with other well-known cases of ant-mediated biocontrol in agriculture, such as with weaver ants (Offenberg 2015), and is, thus far, a limitation of the copious work done on this subject. This apparent lacuna may partially be explained by the difficulties of extracting the impact of ants per se in complex coffee agroecosystems. While long-term comprehensive exclosure studies are needed, these can have cascading impacts on many other predators, such as spiders, anoles, and birds, and failing to control for these impacts can confound exclosure study results (Trager & al. 2010). This may explain the neutral results of one long-term (eight months) coffee ant exclosure study, which did not find a significant impact of ants on coffee herbivores or yield (Philpott & al. 2008d). This experimental approach likely underestimates the impact of ants on plants if it does not account for general trophic shifts in predator communities after ants are removed. This was demonstrated in a meta-analysis of ant-hemipteran-plant interactions, where the authors suggest that natural experiments, which survey plants for ant presence, herbivory, and reproductive output (yield) may be more informative (Trager & al. 2010). Additionally, coffee production studies which artificially increase ant densities on plants, as done in Leefmans (1923), may push the ant-hemipteran trade-off to the negative side, resulting in a net loss in production from increased scale densities. Furthermore, the results of exclosure or survey studies on the impact of ants on coffee plants are ultimately determined by the background levels of herbivores in these systems, such that the long-term benefits of ants may be underestimated if herbivores such as CBB are not particularly common at the study site.

Economic metrics of coffee production are also nuanced. Overall yield on coffee farms is typically determined by both crop quantity and quality (Jha & al. 2014). In cases where ants have potentially negative impacts on quantity, they may still have positive impacts on quality, as they reduce the overall level of CBB infestation in fruits, and fruits with minor CBB damage are sometimes sold at reduced rates (Murphy & Moore 1990). Comprehensive evaluations of ant biocontrol on yield must also consider the costs of other measures to control CBB, such as pesticide use, which is costly, and has external negative impacts on human health where used.

Finally, we must also emphasize the potential for prioritizing both production and conservation in coffee systems where farmers are incentivized to manage farms sustainably through production labeling programs, such as the Smithsonian Bird-Friendly initiative, and through payments for conserving ecosystem services (Jha & al. 2014). In an economic landscape which supports these initiatives, conservation and production can be mutually compatible goals (Jha & al. 2014), and ant conservation biocontrol of CBB may be a model example for sustainable agriculture.

Conclusions and future directions

Here, we summarize evidence that ants on coffee farms antagonize and predate CBB, reduce CBB infestation, and contribute to CBB population suppression. While the general effect of ant diversity on CBB biocontrol is still unknown, evidence shows that both diversity and interaction complexity are important for the overall function of ant-mediated CBB biocontrol. Additionally, ant communities and CBB biocontrol respond to coffee farm intensification on the local and landscape level, where shade and vegetation complexity generally benefits ant-CBB biocontrol, but this effect is context-dependent. Further research is needed to make precise predictions about ant-mediated CBB biocontrol and to improve conservation biocontrol management recommendations. We conclude with several areas of research on this topic that deserve further study.

(1) Broaden geographic scope. Nearly every paper that we reviewed on ant biocontrol of CBB was limited to a handful of countries in the neotropics. While this is a major region of coffee production, some of the most important coffee producing countries are in Southeast Asia and Africa (Jha & al. 2014). To understand the broader benefits of ants for biocontrol in coffee and the potential for their management, investigations should be conducted in other regions. However, we expect many of the benefits outlined here to apply generally to coffee producing regions, as beneficial ant-plant associations are common throughout the world (Styrsky & Eubanks 2007), and diverse ant communities are documented in other coffee regions (Philpott & al. 2008b).

(2) Incorporate potential effects of climate change. It is crucial to consider the impacts of climate change on ant biocontrol of CBB. Some research has suggested that CBB densities may increase in coffee growing regions as warming temperatures expand their altitudinal range and decrease generation times (Jaramillo & al. 2009, 2011). Studies should test the efficiency of ants to suppress CBB under predicted future climate conditions in coffee regions and investigate whether ant biodiversity in farms may provide insurance against climate driven increases in CBB.

(3) Expand work on diversity, ecological complexity, and biocontrol function. To better understand the importance of biodiversity for pest control in coffee, more studies need to be implemented, particularly focusing on the mechanisms involved in ant community function. Increased focus on complex interaction networks in coffee agroecosystems, including ants, other natural enemies, and diverse prey assemblages will help to elucidate the role of biodiversity in pest control function. Furthermore, theoretical work attempting to incorporate interaction complexity into dynamical models will improve our predictive understanding of CBB biocontrol under complex conditions in farms.

(4) Improve mechanistic understanding of local and landscape drivers of ant diversity and biological control. Studies should be designed to target management variables that may help to support ant communities and biocontrol provision. We suggest moving beyond correlative research to manipulative studies which weigh the impact of specific local and landscape variables on ant diversity and function. This may also include augmentation biocontrol studies which investigate techniques for the sustainable manipulation of native ant populations to enhance pest control.

(5) Conduct comprehensive studies on the impact of ants on coffee yields. Expanding on similar work that has been done with other ant biocontrol systems (Offenberg 2015) could reveal the economic impacts of ants in coffee and will help to better evaluate this service. Multiple investigative approaches should be taken, including thorough field surveys and manipulative long-term exclosure studies, to provide a robust understanding of the impact of ants on coffee production and crop quality.

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