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Differential effects of ants as biological control of the coffee berry borer in Puerto Rico

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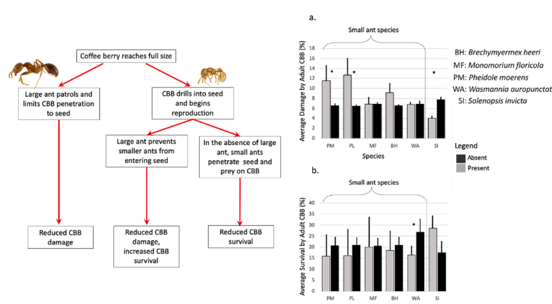
HIGHLIGHTS

- Ants have been shown to be important predators of the coffee berry borer.
- Different species of ants can affect different stages of the coffee berry borer.
- *Solenopsis invicta* reduces damage of berries by preying on CBB outside the berries.
- *Wasmannia auropunctata* can enter the berries and prey on CBB inside the berries.
- *S. invicta* is dominant and can prevent *W. auropunctata* from penetrating berries.

GRAPHICAL ABSTRACT



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ABSTRACT

Conservation biological control consists of managing agroecosystem to maintain and enhance the action of natural enemies. Agroforestry systems such as shaded coffee system has been shown to maintain high diversity of organisms, including predators and parasitoids of insect pest. The coffee berry borer (CBB), *Hypothenemus hampei*, is one of the most widely distributed coffee pests frequently causing severe economic damage. Ants have been reported as natural enemies of the CBB, but different species of ants are known to have different and sometime contrasting effects against the CBB. In this study, we examine the damage and survival of CBB on coffee plants that are dominated by six different species of ants, *Solenopsis invicta*, *Wasmannia auropunctata*, *Monomorium floricola*, *Paratrechina longicornis*, *Brachymyrmex heeri* and *Pheidole moerens*, in Puerto Rico. This represents a novel community of natural enemies since four of the six species are non-native. We hypothesized that the large and dominant species, *S. invicta*, would reduce the damage of the CBB by preying on adult CBB outside the berries, while the smaller species, would reduce the survival of the CBB by preying on the reproducing adults inside the berries (and potentially also on the immature stages, although not quantified in this study). Results show that *S. invicta* was associated with significantly reduced CBB damage. The only species associated with reduced survival of CBB inside berries was *W. auropunctata*, whereas the others were not associated with any effect on survival. Surprisingly, *P. moerens* and *P. longicornis* had a significant positive effect on the damage of the CBB suggesting that these species could only forage on plants that did not harbor *S. invicta* or *W. auropunctata,* the two most aggressive ants both of which were associated negatively with the CBB. The study also suggests that the

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negative impact of *S. invicta* on *W. auropunctata* indirectly facilitates the CBB by protecting it from predation by *W. auropunctata* once the adult CBB gains entrance to the coffee berry.

1. Introduction

It has long been acknowledged that incorporating all complex ecological forces in a biological control program is likely the best way of achieving a truly long-term pest control strategy (Lewis et al., 1997). Part of this strategy consists of maintaining natural enemies of the pest, sometimes referred to as conservation biological control (Barbosa, 1998; Shields et al., 2019). This literature emphasizes the idea that ecosystems are complicated and thus need to be studied carefully, eschewing simplistic popular categories such as the balance of nature and other romantic idealizations. One consistent element of this framework is the idea that multiple natural enemies may provide some measure of "insurance" for biological control, since consequences of the failure of one control agent may be made up by others (Perfecto et al., 2004). The particular element providing the effective biological control is not always obvious (Chaplin-Kramer et al., 2019), is likely to be dependent on other elements in the system, part of the general idea of context dependency (Tylianakis and Romo, 2010).

Ants have long been regarded as potential pest control agents in agroecosystems, in both annual cropping systems (Carrol and Risch, 1990; Drummond and Choate, 2011) and in perennial crops and agroforestry systems (Way and Khoo, 1992; Perfecto and Castiñeiras, 1998), including an effectiveness sometimes thought to emerge from their diversity (i.e., their combined effect) (Gonthier et al., 2013). Here we examine the complexity of such diversity, focusing on a "novel" ecosystem of five ant species (three non-natives and two natives) on two typical coffee farms in the central mountains of Puerto Rico, and its potential to provide effective control of the coffee berry borer (CBB) (*Hypothenemus hampei* Ferrari [Coleoptera: Curculionidae: Scolytinae]), one of the more important pests of coffee world-wide (Damon, 2000; Vandermeer et al., 2002; Infante, et al., 2009). Ants have long been recognized as potential control agents for this devastating pest (Vandermeer et al., 2002; Perfecto and Vandermeer, 2006; Larsen and Philpott, 2010; Jiménez-Soto et al., 2013; Morris et al., 2015, 2018; Morris and Perfecto, 2016). Although the literature is careful to note the highly variable nature of the potential ants have for biological control, depending on the species and surrounding context, popular conceptualizations frequently lump all ants into a single category. Yet direct observations and experiments leave no doubt that different species of ants could have major differences in their biological control potential (Gonthier et al., 2013), and that some ant species interfere with other more effective biological control agents (Eubanks, 2001; Eubanks et al., 2002) and can have a net negative effect on the crop.

In Mexico, there are several small ant species (Hymenoptera: Formicidae) (e.g., *Wasmannia auropunctata* (Roger)*, Pheidole protensa* Wilson*, Solenopsis picea* Emery*, Pseudomyrmex simplex* F. Smith) that can enter the entrance hole of the CBB and thus potentially predate on the eggs, larvae, pupae, and adults inside the fruit (Larsen and Philpott, 2010; Morris and Perfecto, 2016). Other species (e.g., *Azteca sericeasur* Longino*, Pheidole synanthropica* Longino*, Gnamptogenys* sp.) have been seen attacking adult CBB directly, either before they enter the fruit or just as they are exiting (Perfecto and Vandermeer, 2006; Armbrecht and Gallego, 2007; Jiménez Soto et al., 2013), but are much too large to penetrate the entrance hole of the attacked berry, and thus their negative effects can only be felt on adult CBB. This basic morphological difference is compounded by the behavioral characteristic of many ants to tend hemipterans and ward off potential herbivores (including seed predators) in the classic ant/hemipteran mutualism (Zhang et al., 2012). Interspecific competition and aggression among ant species are common, frequently involving the dominance of larger species over smaller ones (Parr and Gibb, 2010). It is common for a large bodied species of ant to be involved in a mutualistic relationship with hemipteran insects, implying a role of protecting the plant from other herbivores (Styrsky and Eubanks, 2010). In the case of coffee, the other herbivores include the CBB (Perfecto and Vandermeer 2006). Even though such a species may consume or otherwise negatively impact adult berry borers seeking to oviposit, it is also likely to reduce or eliminate foraging activity of the smaller ants in the neighborhood. And it is those smaller ants that pose the biggest threat for the immature stages of the CBB (Gonthiers, et al., 2013). Thus, it could be that one ant species (the large body one), although a predator on adult berry borers, acts as an indirect facilitator of the immature stages of the CBB, by providing a refuge where the CBB brood is protected from smaller ant species that can penetrate the seed through the entrance hole constructed by the adult beetle (Gonthiers, et al., 2013). If predation on immatures results in a more effective biological control of the pest, those large body ants involved in the mutualism with hemipterans will effectively be indirectly facilitating the CBB, depending on relative effectiveness of both the large and small-sized ants (Gonthiers et al., 2013; Morris and Perfecto, 2016; Morris et al., 2018).

In Puerto Rico the CBB is regarded as one of the most important pests in the coffee system (Bayman et al., 2021), and farmers have little hope for establishing effective management systems (personal communication with farmers). The most active ants on Puerto Rican coffee farms consists mainly of two large ants (*Solenopsis invicta* Buren, and *Paratrechina longicornis* Latreille) and several smaller species (*Wasmannia auropunctata* Roger*, Tapinoma melanocephala* [Fabricius]*, Brachymyrmex heeri* Forel, *Pheidole moerens* Wheeler, and *Monomorium floricola* [Jerdon]), assembled in a "novel" community (all, except *B. heeri* and *P. moerens* are non-native species) (Perfecto and Vandermeer, 2015; 2020;; Vandermeer and Perfecto, 2020). Given the above scenario, we hypothesize that the dominant species *S. invicta* acts effectively and indirectly as a promotor of the CBB, by reducing the predatory activity of the smaller species (especially *W. auropunctata*, which is predominant among the smaller species) on the immature stages of the CBB inside the coffee berries (Fig. 1). We engaged in a detailed study on two farms in the central/west cordillera, the coffee-growing region, of Puerto Rico, seeking evidence that this indirect effect is operative. Our hypothesis is that S. *invicta*, restricts the access of the other, smaller, ants to the coffee fruits, and thus has an indirect positive effect on the survival of the CBB inside the berries, even as it restricts the adult berry borers from entering the fruits in the first place (Fig. 1). We devised a census methodology with specific predictions to determine whether predicted correlations between indicator metrics concorded with our predictions.

2. Methods and materials

The study took place in the Utuado municipality of Puerto Rico, on two farms, Finca Cítricos (elevation 430 AMSL, code UTUA13 in Perfecto and Vandermeer, 2020; lat = 18.279491, long = 66.828209) and Finca Gran Batey (395 AMSL, code UTUA3, lat = 18.287858; long = 66.770264) during July 2019, at a time when fruits were in the late process of ripening, when most of the attacks of the CBB had already taken place. Both farms are <20 ha and have coffee interspersed with other species, such as citrus, banana, plantain, breadfruit, and a variety of root crops. Pesticides have not been sprayed for at least two years prior to the study, although before that they may have been used. Neither farm is identified by its owner as organic. Both farms have interspersed shade trees, plantains, and root crops. UTUA3 has many citrus trees intercropped with the coffee. We mapped the distribution of ant species on coffee plants in an area of 2500 m^2 in Finca Gran Batey and 1950 m^2 in Finca Cítricos, Inc., by placing tuna baits, a small dollop of approximately one cm^2, on each of five branches evenly distributed from the topmost to the lowermost branches, on each coffee bush. *Wasmannia auropunctata*, the little fire ant, and *Solenopsis invicta,* the red imported fire ant, were the ants with the highest levels of activity (number of baits occupied per coffee plant) and occupancy (number of coffee plants occupied by this species) on both farms. Other ant species with relatively high occupancy were *Pheidole moerens*, *Brachymyrmex heeri*, *Patratrechina longicornis*, and *Monomorium floricola,* all of which, except *P. longicornis*, are of small size and can penetrate the coffee berry through the entrance hole of the CBB (direct observation by I. Perfecto and J. Vandermeer).

Using the ant survey data, subsamples were taken by numbering coffee plants within a section of the mapped plots and randomly selecting plants for CBB damage evaluation. Each randomly selected coffee plant was sampled by haphazardly selecting three branches originating from a main stem, at high, medium, and low positions on the plant. For each branch, the total number of berries and number of CBB-damaged berries were counted. CBB-damaged berries were collected in plastic bags for further examination in the laboratory, using a dissecting scope. Bagged fruits were examined in the laboratory within 24 h after collection, and bags were examined for adult CBBs that may have escaped the fruits in transport (none were found). Coffee plants with few to no berries, plants with berries out of reach, and berries less than two centimeters in length were excluded from the data. A total of over 20,000 berries were assessed on 430 coffee plants in UTUA3 and 252 in UTUA13.

Our methods depend on the well-known fact that frequently CBB-damaged fruits do not contain borers and that numerous ant species actively remove adults from fruits that they are in the process of boring (Jiménez-Soto et al., 2013). During that process they leave a scar that, from the outside appears to be an attacked fruit, even though the attack had been interrupted by some agent before the beetle could enter and do extensive damage. Thus, by dissecting “damaged” fruits (those with evident external damage), it is possible to categorize those in which the beetle adult had been successful in entering, and those in which it had not been successful. A fruit that had external damage, but no beetle inside, can be presumed to have been removed by something, in the case of this study, probably an ant. Of course, the beetle could have just decided to leave the fruit after boring into it, but we think this unlikely.

Collected berries were cut cross-sectionally and placed in one of two categories, 1) “damaged” (clearly bored but with no living CBB inside), and 2) “survival” (living adult CBB encountered inside the berry). Both the “damaged” and the “survival” categories were either in an AB (no penetration of endosperm) or CD (penetration of endosperm) condition, with the main distinction being the presence or absence of the adult beetle inside the berry. Following opening berries and classifying them, berries and their contents were frozen (in a commercial freezer) for at least four hours and then discarded. Percent CBB damage per plant was calculated as the number of “damaged” berries per plant divided by the total number of berries on that plant, times 100; percent CBB survival per plant was calculated as the number of berries with surviving adult CBB divided by the total number of damaged berries, times 100. The six most abundant ant species (either in terms of activity or number of bushes occupied) were analyzed separately for the effect of ant species on the CBB. The effect of individual ant species on CBB damage and survival was analyzed by comparing damage and survival proportions on plants with a particular ant species to plants without that species using a simple resampling protocol with 1000 resamples and calculating the p value as the fraction of 1000 fitting within the observed difference. All analyses were done both for data pooled from both farms and for individual farms.

3. Results

A cumulative total of 15 species of ants were observed in the study, with more species found in Finca Gran Batey (13 species) than in Finca Cítricos, Inc. (8 species) (Table 1). The six most abundant species were, *Wasmannia auropunctata*, *Solenopsis invicta*, *Monomorium floricola*,

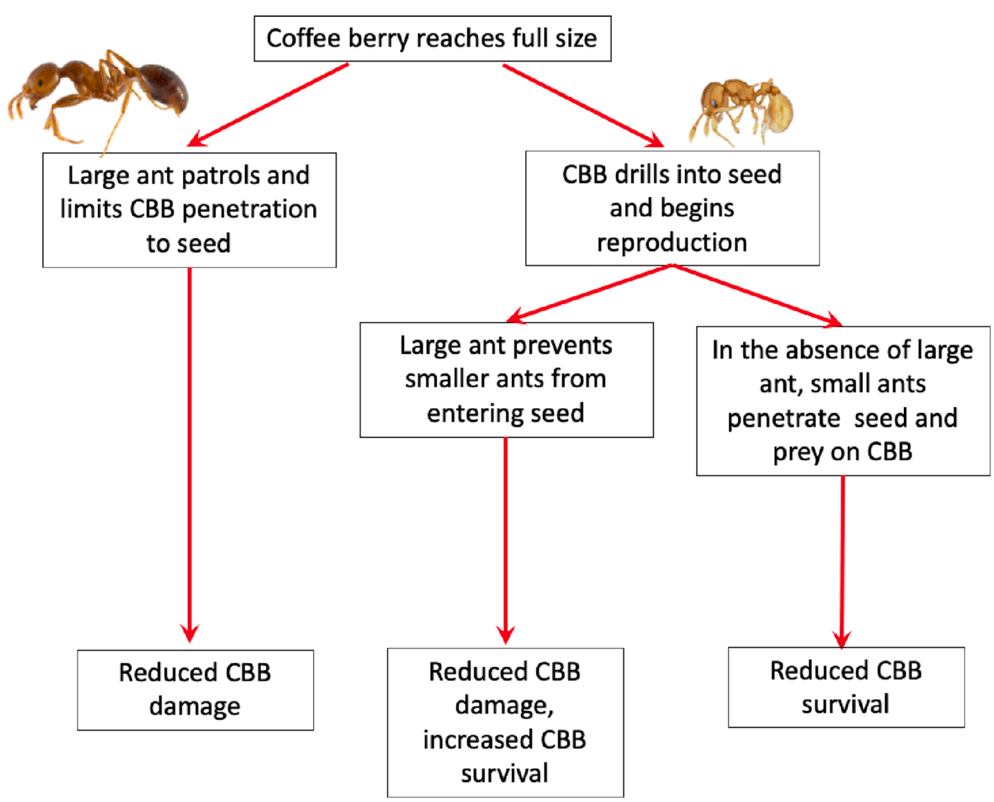

Fig. 1. Basic expectation under the hypothesis that larger ants have an indirect positive effect on the CBB, exerted by preventing the smaller ants from entering the berries and preying on the CBB inside the berries.

Table 1
Ant prevalence (proportion of coffee bushes containing a given species) in Finca Gran Batey and Finca Cítricos, Inc. (bolded species are the ones analyzed in this study).

Ant Species	Finca Gran Batey	Finca Cítricos, Inc.
Brachymyrmex heeri	17%	6%
Brachymyrmex obscurior	5%	–
Dolichoderine sp.	1%	–
Monomorium floricola	9%	11%
Nylanderia pubens	4%	1%
Nylanderia stenheili	–	1%
Paratrechina longicornis	13%	–
Pheidole exigua	1%	–
Pheidole megacephala	2%	–
Pheidole moerens	13%	–
Pheidole sp.	1%	1%
Solenopsis invicta	9%	79%
Solenopsis sp.	3%	–
Tapinoma melanocephala	–	5%
Wasmannia auropunctata	81%	31%
Overall number of species	**13**	**8**

Pheidole moerens, *Paratrechina longicornis*, and *Brachymyrmex heeri*, however *P. moerens* and *P. longicornis* were not observed in Finca Cítricos, Inc. Reported results are for these six most prevalent ant species. The species richness per plant was regressed against the percent CBB damage and survival but did not prove to be a significant variable impacting either one of these variables and is thus not presented here.

Pooled data for both farms shows an average CBB damage per plant at 6.4% (±8.1) and average CBB survival per plant at 23% (±32.5), (averages and their standard deviations were calculated using traditional equations). As expected, *S. invicta* had a significant negative effect on CBB damage (Fig. 2a). The general hypothesis that the smaller ants will influence "survival" is not supported – we find no effect on either damage or survival relative to presence or absence of the small species. However, in a species-by-species comparison (those common enough to be analyzed) we find general support for our hypothesis with *W. auropunctata* (Fig. 2b), while the other small species show variable responses. Thus, *S. invicta* reduces damage by CBB, while *W. auropunctata* reduces survival of the CBB once they enter the berries (Fig. 2).

A notable exception to the expected pattern is presented by *P. moerens* and *P. longicornis*, as well as the trend, albeit nonsignificant of *B. heeri*. Damage of the CBB is significantly higher in the presence of *P. moerens* and *P. longicornis,* and higher but not significantly in the presence *of B. heeri* (Fig. 2a). It is evident from field observations that these three species are subdominant to the two very aggressive dominants *W. auropunctata* and *S. invicta*. The absence of the latter two species, coupled with the evidence that both tend to reduce CBB damage or survival, suggests that the apparent promotion of CBB damage by the three smaller ants is simply an indirect consequence of their inability to forage on plants that are dominated by one or the other of the two dominant ants that do reduce damage and survival. Perhaps this is speculative, but it is consistent with the data collected.

There is significant variability from farm to farm. Separating the two farms, we see that the Gran Batey farm is basically driving the pooled data patterns, while the variability at the Cítricos farm effectively reduces the degree of significance in the pooled data, as easily seen in Figs. 3 and 4. The data from Finca Gran Batey also show that (Fig. 3). It is important to note that while the positive effect of *S. invicta* on the survival of the CBB was not significant for the pooled data (Fig. 2b), it was significant for Finca Gran Batey; the presence of *S. invicta* significantly increases the percent survival of the CBB inside the berries, as we predicted.

4. Discussion

Despite literature claiming the efficacy of diverse ant communities in controlling CBB, we find that the identity of the potential control agents (ants) was far more important than generalized measures such as species richness. We found that the presence of *S. invicta* in coffee plants significantly reduce the damage of the CBB, while the presence of *W. auropunctata* significantly reduces the survival of those CBB that manage to penetrate the berries. Although our conclusions were based on inferences, other studies that have done exclusions of ants, have found similar results (Gonthier et al., 2013; Morris et al., 2015). Furthermore, a general knowledge of the natural history of these two species enabled a sensible hypothesis formulation, based on other studies, and our field observations support that hypothesis. The basic story is like that reported for a similar situation in Mexico (Vandermeer et al., 2019) in which a large and aggressive ant species, too large to enter the tunnel made by the CBB, effectively repels the CBB adults while searching for a place to borrow or while borrowing into the berry, and thus reduces its damage. Yet one or more ant species small enough to enter the berry through the hole made by the CBB when it entered, are

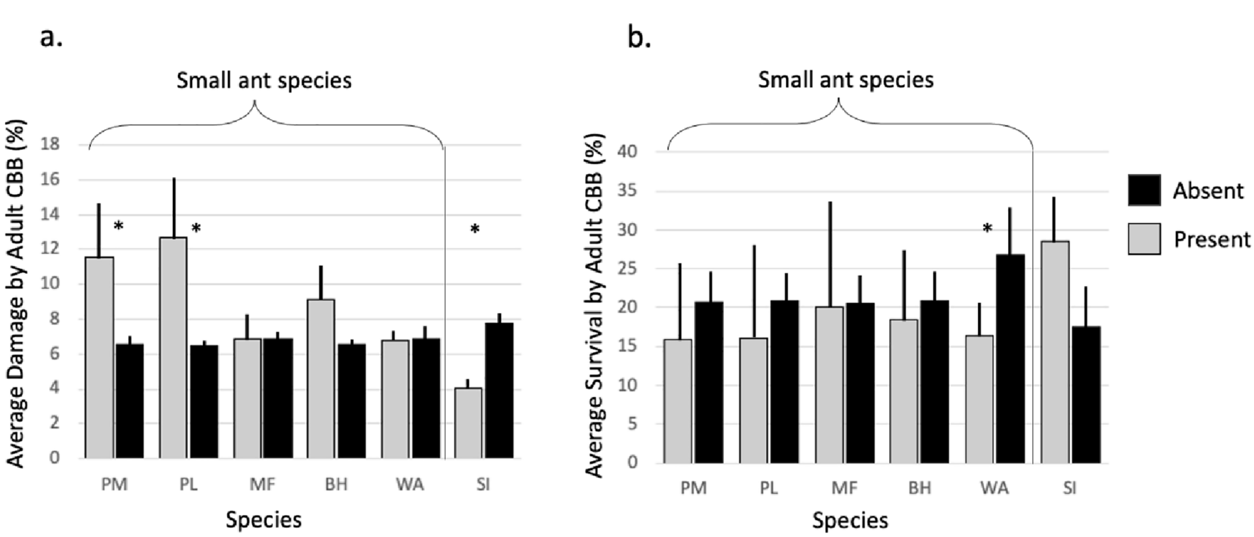

Fig. 2. Effect of presence and absence of individual ant species on average percent damage by adult CBB (a.), and average percent survival of adult CBB (b.) pooled over both farms sampled (PM = *Pheidole moerens*, PL = *Paratrechina longicornis*, MF = *Monomorium floricola*, BH = *Brachymyrmex heeri,* WA = *Wasmannia auropunctata*, and SI = *Solenopsis invicta*). Error bars represent standard error; * represents a p value of < 0.05.

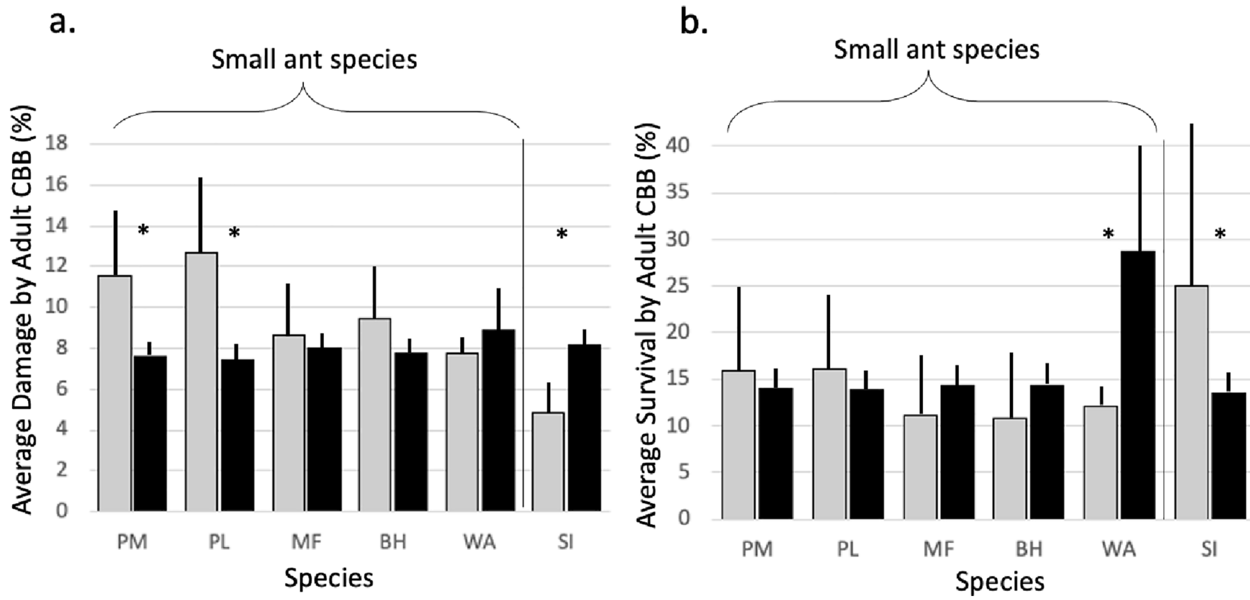

Fig. 3. Effect of presence and absence of individual ant species on average percent damage by adult CBB (a.), and average percent survival of adult CBB (b.) in Finca Gran Batey (PM = Pheidole moerens, PL = Paratrechina longicornis, MF = Monomorium floricola, BH = Brachymyrmex heeri, WA = Wasmannia auropunctata, and SI = Solenopsis *invicta*). Error bars represent standard error; * represents a p value of < 0.05.

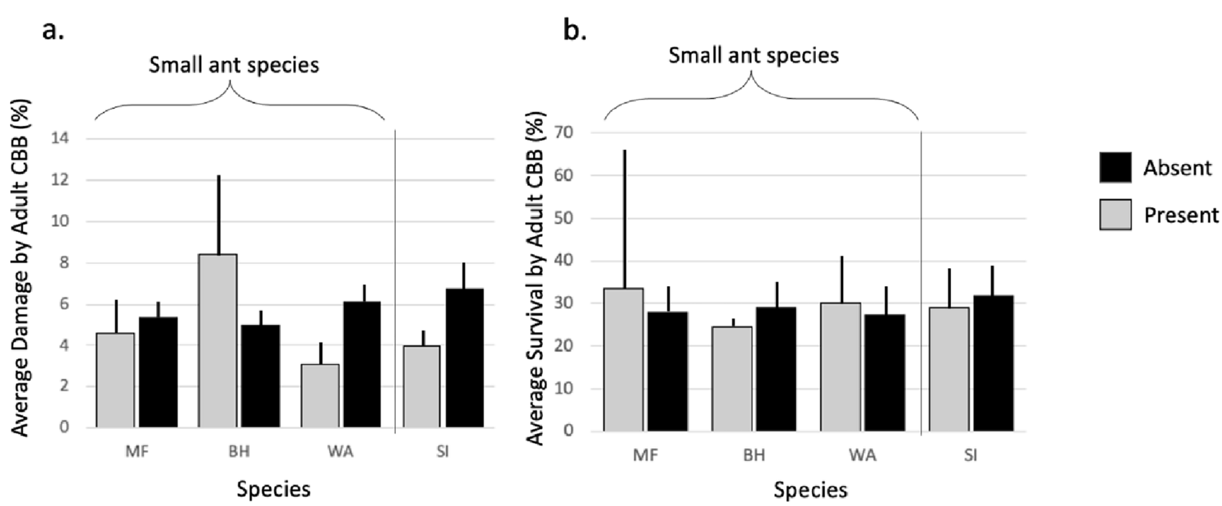

Fig. 4. Effect of presence and absence of individual ant species on average percent damage by adult CBB (a.), and average percent survival of adult CBB (b.) in Finca Cítricos, Inc. (MF = Monomorium floricola, BH = Brachymyrmex heeri, WA = Wasmannia auropunctata, and SI = Solenopsis *invicta*). Error bars represent standard error; * represents a p value of < 0.05.

effective at predation inside the berry. However, the CBB inside the berries on plants that are patrolled by the larger species face lowered predation due to the protection offered by the larger species reducing the foraging effectiveness of the smaller species. Thus, the larger species, in the case of this study, *S. invicta*, can acts as an agent of biological control by reducing the direct attack of the pest, while the smaller species, *W. auropunctata*, can acts as an agent of biological control by reducing the CBB inside the berries, even though not effective at preventing the pest attack in the first place (Fig. 1). Furthermore, there is an important indirect effect as suggested in the introduction, in that a plant dominated by *S. invicta* apparently reduces the activity of *W. auropunctata*, thus effectively protecting the CBB and its brood when it is inside the berry. *S. invicta* thus simultaneously reduces pest attack while at the same time increases the survivorship of the pest once it is inside the seed. It is also important to note that while *S. invicta* reduces the attack to berries, enough numbers of CBB females can escape predation reducing the effectiveness of this species as a biological control agent.

Further implications of this interaction include yet another indirect effect. Vega et al. (2011) have shown that there is extensive intraspecies competition among immatures of the CBB, to the extent that one might even expect a dramatic "stunting" effect at high pre-adult densities within coffee fruits. Too many individuals in a single berry, in the absence of cannibalism, may eliminate all available resources before any of them can mature, thus creating a very strong density dependence effect. The small ants, in this scenario, could thus have a net positive effect by "thinning" the pre-adult populations. Thus our "reduced CBB survival" of Fig. 1 would have to be modified to consider this important higher order effect.

Both *S. invicta* and *W. auropunctata* also forage on the ground and can potentially have similar impacts on the CBB that remain within the berries that fall to the ground during harvest. It is well known that CBB survive and continue reproducing in the berries that are left on the plants or on the ground after harvest and represent an important source of new infestation early in the following season. The same dynamic that is described in this study could be operative on the ground with the exception that the positive effect of *S. invicta* on free roaming adults would be possible only when the CBB adults are emerging from the berries to find new fresh berries to oviposit. On the other hand, the effect of *W. auropunctata* could be important in reducing not only the adults that are inside the berries through the entire time that the berries remain on the ground, but also, they could prey on the brood (Morris and Perfecto, 2016), potentially reducing the number of emerging females early in the season.

Interestingly, Rodríguez et al. (2013) speculate that the importance of this pest species, especially in coffee monocultures, is a consequence of its evolutionary background in Africa, in which the production of large numbers of females is an evolutionary response to the need for large numbers of females to locate the scattered patches of suitable aged berries that existed during its evolution. The importance of the ant/hemipteran mutualism within this evolutionary framework is interesting, in that the evolutionary pressure would have included not just the scattered patches of suitable berries, but the availability of the ant "protectors" given the results suggested herein. That is, it is conceivable that what we see in the Americas, even though we are dealing with novel ecosystems (that is, coevolution in situ is virtually impossible), is a consequence of direct evolutionary pressures, involving ants that tend hemipterans.

5. Conclusion

The two predominant ants in the system, *W. auropunctata* and *S. invicta*, despite being invasive species and considered nuisance pests because of their painful stings and tendency to form monospecific patches (Adkins, 1970; Wetterer and Porter, 2003), can play important and complementary roles in the biological control of the CBB. While *S. invicta* attack the CBB adults outside the berries, *W. auropunctata*, can penetrate the berries and attack the CBB adults and brood inside the berries. However, *S. invicta* also prevents *W. auropunctata* from foraging on plants where they are dominant and can provide protection against *W. auropunctata* predation on those CBB that manage to enter the berries within those plants, therefore increasing their survival.

This study highlights the complications of using ants as biological control of the CBB. Although the results strongly suggest that ants are preying on the CBB inside and outside the berries, we still don't know what the net effects of these two species on coffee yield are, especially in the context of the nuisance that these two species represent for coffee harvesters.

CRediT authorship contribution statement

Jannice Newson: Conceptualization, Methodology, Data curation, Visualization. **John Vandermeer:** Conceptualization, Methodology, Writing - review & editing. **Ivette Perfecto:** Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

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

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