

ARTICLE

An aggressive nonconsumptive effect mediates pest control and multipredator interactions in a coffee agroecosystem

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Handling Editor: Juan C. Corley**Abstract**

Natural pest control is an alternative to pesticide use in agriculture, and may help to curb insect declines and promote crop production. Nonconsumptive interactions in natural pest control that historically have received far less attention than consumptive interactions, may have distinct impacts on pest damage suppression and may also mediate positive multipredator interactions. Additionally, when nonconsumptive effects are driven by natural enemy aggression, variation in alternative resources for enemies may impact the strength of pest control. Here we study control of the coffee berry borer (CBB), *Hypothenemus hampei*, by a keystone arboreal ant species, *Azteca sericeasur*, which exhibits a nonconsumptive effect on CBB by throwing them off coffee plants. We conducted two experiments to investigate: (1) if the strength of this behavior is driven by spatial or temporal variability in scale insect density (an alternative resource that *Azteca* tends for honeydew), (2) if this behavior mediates positive interactions between *Azteca* and other ground-foraging ants, and (3) the effect this behavior has on the overall suppression of CBB damage in multipredator scenarios. Our behavioral experiment showed that nearly all interactions between *Azteca* and CBB are nonconsumptive and that this behavior occurs more frequently in the dry season and with higher densities of scale insects on coffee branches. Our multipredator experiment revealed that borers thrown off coffee plants by *Azteca* can survive and potentially damage other nearby plants but may be suppressed by ground-foraging ants. Although we found no non-additive effects between *Azteca* and ground-foraging ants on overall CBB damage, together, both species resulted in the lowest level of plant damage with the subsequent reduction in “spillover” damage caused by thrown CBB, indicating spatial complementarity between predators. These results present a unique case of natural pest control, in which damage suppression is driven almost exclusively by nonconsumptive natural enemy aggression, as opposed to consumption or prey behavioral changes. Furthermore, our results demonstrate the variability that may occur in nonconsumptive pest control interactions when natural enemy aggressive behavior is impacted by alternative resources, and also show how these nonconsumptive effects can

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mediate positive interactions between natural enemies to enhance overall crop damage reduction.

KEYWORDS

ants, coffee, coffee berry borer, crop damage, multipredator interactions, natural enemy aggression, natural pest control, nonconsumptive effects

INTRODUCTION

With the increasing alarm surrounding global insect declines (Hallmann et al., 2017; van Klink et al., 2020; Wagner, 2020), a prescription that continues to emerge is the need for drastic reductions in pesticide and insecticide use (Harvey et al., 2020; Kremen & Merenlender, 2018), which appears to be one of the major drivers of the observed declines (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). Natural pest control, through the conservation of natural enemy habitat in agricultural landscapes, can serve as an alternative to promote the production of crops, the regulation of pests, and the conservation of biodiversity (Bianchi et al., 2006; Dainese et al., 2019; Karp et al., 2013). One of the challenges to this approach is understanding how diverse communities of natural enemies impact the overall functioning of pest regulation (Casula et al., 2006; Griffin et al., 2013; Letourneau et al., 2009; Straub et al., 2008). However, in focusing primarily on the relationship between predator richness and pest control, this research often overlooks the complexity of interactions between predators and pests that serve as the ultimate mechanisms for pest suppression (Crowder & Jabbour, 2014). When interactions are studied in pest control, most often, direct, consumptive interactions receive the bulk of the attention (Eubanks & Finke, 2014). This is despite the growing awareness of the ubiquity of trait-mediated and nonconsumptive interactions in communities, which, more generally, have been shown to have impacts of equivalent magnitudes on prey regulation (Preisser et al., 2005; Werner & Peacor, 2003) and plant communities through trophic cascades (Schmitz et al., 2004).

In pest control, nonconsumptive effects of natural enemies can increase pest risk and reduce pest damage by magnitudes comparable with consumptive interactions (Eubanks & Finke, 2014; Hermann & Landis, 2017; Thaler & Griffin, 2008). These interactions can have effects on pest populations that are disproportionate to the density of natural enemies, potentially serving as mechanisms for the influence of keystone biocontrol agents (Meadows et al., 2017). This may occur when the mere presence of natural enemies changes the behavior of prey to reduce pest feeding rates, although not necessarily impacting pest densities

themselves (Eubanks & Finke, 2014). Importantly, nonconsumptive effects can also mediate the interactions between natural enemies (Davenport & Chalcraft, 2013) and may potentially influence the impact of natural enemy diversity on pest control (Ingerslew & Finke, 2018; Meadows et al., 2017). When enemies compete directly over shared prey resources or space, multipredator interactions often have negative impacts on prey regulation, but when predators are spatially separated or functionally distinct, nonconsumptive effects can result in positive synergistic pest regulation (Ingerslew & Finke, 2018; Meadows et al., 2017).

A particularly interesting example of this was documented by Losey and Denno (1998), in which they showed that the presence of a Coccinellid predator on plants caused aphids to drop to the ground, making them more available to a ground-foraging beetle (Losey & Denno, 1998). This study demonstrated how the spatial separation of predators on plants and the ground, along with the nonconsumptive effect of one of the predators on the pest, enhanced overall control and resulted in positive synergistic multipredator effects (Losey & Denno, 1998). Other research on aphid dropping in multiple wasp enemy communities has found more conflicting results, in which consumptive effects between enemies resulted in interference and reduced overall prey suppression, but nonconsumptive effects yielded positive additive prey suppression (Ingerslew & Finke, 2018). Despite this research, few studies have explored the importance of nonconsumptive interactions in multienemy pest control scenarios, in which impacts on crop damage are explicitly tested (Hermann & Landis, 2017). Furthermore, the dynamics of nonconsumptive interactions are not well understood in pest control, and few studies have tested how nonconsumptive enemy behavior changes across space or time (Hermann & Landis, 2017; Sheriff et al., 2018), despite the long history of dynamical research on consumptive predator-prey interactions. This may be particularly important when nonconsumptive effects are driven by predator aggression, as opposed to prey behavioral responses, and spatial or temporal variation in alternative resources for predators impacts the strength of nonconsumptive effects, potentially resulting in variable or inconsistent pest damage suppression.

In shaded coffee agroforests, communities of natural enemies can be quite diverse, leading to a host of potential multipredator interactions and nonconsumptive effects (Perfecto et al., 2014; Vandermeer et al., 2010, 2019). Ants have received much attention in the coffee pest control literature, particularly in Latin America, where some species are known natural enemies of the coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari 1867), (Morris et al., 2018; Philpott & Armbrecht, 2006), a major global pest of coffee, which bores into fruits and significantly reduces yield. In southern Mexico, the ecology of the arboreal ant, *Azteca sericeasur* (Longino 2007), has been investigated extensively for its apparent keystone role in the interaction networks of coffee farms (Vandermeer et al., 2010, 2019). It is well documented that this ant suppresses the damage of CBB, in both the laboratory (Pardee & Philpott, 2011; Philpott et al., 2012), and in the field (Gonthier et al., 2013; Jiménez-Soto et al., 2013; Morris et al., 2015). This species is commonly observed foraging on coffee bushes in this region where it tends hemipteran insects (scale) for honeydew. When *Azteca* ants participate in these mutualistic relationships with scale, they can indirectly benefit coffee by patrolling plants and preying on other herbivores that might threaten the supply of honeydew resources from their scale partners (Morris et al., 2018; Perfecto & Vandermeer, 2006). However, this behavior may also drive nonconsumptive interactions with coffee herbivores, including CBB. This has been observed previously, when *Azteca* ants will attack CBB individuals during their colonization of coffee plants, often throwing or pushing them off plants to the ground (Jiménez-Soto et al., 2013). Unlike many other cases of nonconsumptive enemy–prey interactions (Hermann & Landis, 2017), this effect appears to be driven by the enemy’s antagonistic, but nonconsumptive impact, and not by a behavioral response of the prey.

Despite this aggressive behavior, it is still not well understood what the overall impact of this nonconsumptive interaction is on coffee pest control. Previous work in this system has reported conflicting frequencies of this behavior compared with direct consumption of CBB (Jiménez-Soto et al., 2013; Perfecto & Vandermeer, 2006). Variability in the intensity of this interaction or in the proportion of nonconsumptive to consumptive interactions by ants may have important impacts on the dynamics and efficacy of pest control in this system. Interestingly, because this nonconsumptive interaction is driven by enemy aggression, rather than prey defense, these dynamics may be governed by the availability of honeydew resources for ants from scale insects on coffee, which previous research suggests may influence *Azteca*’s reduction of CBB damage (Rivera-Salinas et al., 2018). Although it is not always clear how honeydew availability (Clark & Singer, 2018) or hemipteran

insect density (Kaplan & Eubanks, 2005) influences ant–plant defensive interactions more generally, research on other species of *Azteca* ants in this region has demonstrated that seasonal variability in plant carbon pools may impact scale insect honeydew and the strength of ant–plant defense (Pringle et al., 2013). Furthermore, it is not clear what impact this nonconsumptive effect has on overall CBB damage and the broader control of coffee pests in the community, where the flux of resources from coffee plants to the ground may mediate interactions between *Azteca* and other ground-foraging predators, potentially resulting in enhanced control of pests and positive multipredator effects.

To assess these questions and gain an understanding into the natural history of this complex pest control interaction, we conducted both a field behavioral experiment and a laboratory multipredator experiment. With our behavior experiment, we aimed to test (1) if the strength of *Azteca*’s aggressive nonconsumptive effect on CBB varies positively across space (on coffee) or time (between seasons) with the density of scale insects (an alternative resource). With our laboratory experiment we aimed to understand (2) how this behavior impacts overall CBB damage in multipredator communities and (3) if CBB throwing results in positive interactions or spatial complementarity between *Azteca* and ground-foraging predators. Ultimately, we aimed to illuminate how this unique nonconsumptive effect, driven by the aggressive behavior of a dominant keystone consumer, influences the overall regulation of this important agricultural pest.

METHODS

To understand the impact of the nonconsumptive interaction between *Azteca sericeasur* and CBB on pest control we conducted two experiments. First, we performed a behavioral experiment in the field to investigate variability in the strength of this nonconsumptive interaction, regarding the availability of scale insect resources for *Azteca* across space on coffee bushes and time between seasons. Second, we conducted a laboratory experiment to assess the impact of this behavior on borer damage in multipredator scenarios and to understand how this nonconsumptive effect mediates interactions between *Azteca* and ground-foraging predators. All experiments were conducted at Finca Irlanda in Chiapas, Mexico. The farm is a 300-hectare, certified organic, shaded coffee poly-culture situated at roughly 1000 m elevation at 15°11' N, 92°20' W. Data for the behavioral experiment were collected during July 2019 and February 2020, whereas data for the multipredator experiment were collected during October 2016.

Field behavior experiment

To assess the variability of this nonconsumptive behavior in the field we conducted a behavioral assay. We haphazardly selected 20 sites where *Azteca sericeasur* ants were active on coffee bushes. We chose sites that were separated by a minimum of 6.13 m (between ant nest host trees) to increase the likelihood that ants from each site represented different colonies from different shade trees, however the average distance between sites was roughly 43 m. We measured the activity of ants on coffee by counting the number of individuals crossing a fixed point on the central trunk of the coffee bushes for 1 min. We selected one coffee bush at each site with at least five individual ants observed during the 1-min period. Then, we selected one branch on each coffee plant and measured the branch-level ant activity by visually scanning the branch and counting all individuals. We chose branches that had a minimum of three ant individuals for our experiment. Finally, we estimated the availability of resources for *Azteca* ants from scale insects by counting the number of adult scale insects on branches of a few common species, including the green coffee scale, *Coccus viridis*. On one coffee bush replicate some aphid individuals were also being tended by ants and were included in our count of scale, although this did not statistically alter our results.

To assess the variability of borer throwing by *Azteca*, we placed individual live adult borers on coffee plants and recorded the resulting behavior of *Azteca* ants. Adult borers were extracted from bored green coffee fruits collected in the field. For each behavioral trial, borer individuals were placed on a leaf of the chosen branch of coffee plant replicates and observed for up to 3 min. We recorded three possible outcomes from these trials. First, we recorded “consumption events” when *Azteca* ants encountered borers, captured them, and returned to the ant foraging trail on the trunk of the coffee plants (which we assumed indicated that the ants were bringing borers back to their nest). Second, we recorded the nonconsumptive dropping behavior when ants interacted with borers by capturing them and dropping them from leaves or by pushing them off leaves, in either case resulting in the removal of the borer from the coffee plant. Finally, if ants encountered borers but did not remove them or if ants failed to encounter borers, we recorded the result as a non-interaction. Because we were only interested in the overall rate of borer throwing in this study, and other studies have reported more on the details of ant–borer behavioral interactions (Jiménez-Soto et al., 2013), we chose to simplify our interaction outcomes into these three principal categories. The time of all interactions was recorded and if no interaction

occurred, we recorded the end time of the trial at 3 min. We repeated behavioral trials five times per bush on the same branches to estimate the frequency of borer throwing per each site using new CBB individuals for each replicate.

To test for variability in the proportion of borers thrown by ants due to resource variability by season, we conducted this experiment in two different seasons. First, during the rainy season in July 2019, when scales insects are typically considered to be more abundant and then in February 2020, during the dry season, when there are typically fewer arthropods, including hemipterans (Williams-Guillén et al., 2008). Local precipitation at the farm varied significantly between these sampling points, with 249 mm rainfall measured during July 2019 and 43 mm during February 2020, indicating that these sampling periods represent distinct seasons. In most cases, the trials were repeated at the same sites for both sampling periods and on the same coffee bushes. When this was not possible due to low ant activity during the second sampling in the dry season, we substituted another nearby bush with sufficient *Azteca* activity at the same site, or in four cases a new site was chosen. Only 19 site replicates were used during the dry season.

To test if season or scale insect density on branches drove differences in the frequency of nonconsumptive behavior by *Azteca*, we conducted a generalized linear mixed model (GLMM). We included season as a categorical fixed effect, branch-level scale density as a continuous fixed effect, and their interaction as a fixed effect, as well as site as a random effect (to control for spatial non-independence between repeated replicates on the same plant). We modeled behavioral outcomes using a binomial error distribution and logit link function (outcomes were reduced to two possible types: nonconsumptive throwing or no interaction given the lack of observed consumption; please refer to the section [Results](#)). To assess whether there were differences in scale insect abundance on coffee branches between seasons we conducted a generalized linear model (GLM). We included the sampling time (season) as a fixed effect and ran the GLM using a Poisson error distribution with a log link function, to account for count data.

Multipredator interaction experiment

To better understand the impact of *Azteca*'s nonconsumptive effect on CBB damage reduction in multipredator communities we conducted an additive, fully factorial laboratory experiment with two predators. We designed mesocosms in the laboratory using coffee plant saplings (Figure 1). Mesocosms included four different



FIGURE 1 Experimental setup of multipredator interaction mesocosms.

treatments: a control with no ants, an *Azteca*-only treatment, a ground-foraging ant treatment, and a treatment with both ant species. We used the ant species *Wasmannia auropunctata* (Roger 1863) as the ground-foraging species, because it is a known predator of CBB (Gonthier et al., 2013; Newson et al., 2021) and can be easily collected and manipulated in the laboratory. Coffee plants were acquired from the nursery at Finca Irlanda and were all *Coffea arabica* individuals of the same variety and age. All plants were roughly 70 cm tall and were watered every 2–3 days in the laboratory. Plants were placed in 70-cm diameter plastic washtubs and were kept in plastic containers to avoid water or dirt from spilling into the mesocosms. A coating of fluon was applied to the sides of tubs to keep ants and borers from escaping mesocosms (although some borers could potentially fly out). Additionally, fluon was applied to the outside of plant containers and tanglefoot to the base of coffee plants to avoid the direct interaction of the different ant species. We chose to limit direct ant interactions because of the artificial proximity of the ants in our mesocosms (on small coffee saplings) and the potential for this to unnaturally amplify ant aggression by reducing the amount of territory that multiple ants would typically share in the field. In total, 10 tubs and 20 coffee saplings were used throughout the experiment. For treatments with *Wasmannia* ants, ants were placed on the floor of washtubs and kept in open plastic containers along with

pieces of moss, plants, and twigs collected during ant collection in the field to provide temporary shelter and suitable microclimatic conditions (Figure 1). For treatments with *Azteca* ants, ants were placed directly on coffee bushes. A small drop of honey was placed on five leaves of each coffee plant to simulate the honey dew resources provided by scale insects for *Azteca* ants. Roughly 40 individuals of *Azteca* were placed on bushes. For *Wasmannia* treatments, we filled ant containers with a minimum of 100 individuals, although this number is likely to vary substantially between replicates due to the difficulty in counting such small ants. These densities of ants were chosen given our observations of what was typical for these species in the field. We used the same number of ants for the treatment with both ant species as for individual treatments to conduct an additive experiment. We used this design to directly test for non-additive effects from the interaction of ants on borer control, assuming that the resulting borer damage measured from the treatment with both ants would differ from the sum of that of the individual ant treatments, if a synergistic or facilitative interaction occurs (Cardinale et al., 2003).

All ants were collected in Finca Irlanda and stored in plastic containers with perforated lids between trials. *Azteca* ants were collected from different nest trees separated by a minimum of 5 m for different replicates. Both majors and minors of *Azteca* were collected along with fragments of carton nest material. *Wasmannia* ants and brood were collected by scraping epiphytes and bark from trees and from hollowed out branches collected from the ground. Although *Wasmannia* ants in the area of the study may exist in large “supercolonies” spread out across farms (Yitbarek et al., 2017), we attempted to collect from different areas separated by at least 2 m for each replicate. All ants were kept in containers in the laboratory until the morning of experimental trials, but no longer than 1 week. In two instances some ants were reused to supplement *Wasmannia* colonies with low activity.

Because coffee saplings were too young to produce fruits, we collected fruits from plants in the field to add to our mesocosms. We added branches with 20 unbored fruits to plants in the laboratory by positioning them across branches of the saplings and added 20 unbored individual green coffee fruits on the floor of mesocosms (Figure 1). Fruits were placed both on coffee plants and on the ground to track individual borers and borer damage in both places. Branches that were added to coffee plants had all leaves removed and any additional fruits until each branch had exactly 20 unbored fruits. Fruits and coffee plants were arranged in experimental mesocosms at least 2 h before beginning trials with ants and borers to allow plant volatiles to dissipate.

At the start of each experimental trial 40 individual CBBs were placed on the coffee plants in our mesocosms. We chose this density to more easily track CBB damage given the possibility that some borers may die or escape in the laboratory, but this density has been also frequently observed on individual plants in the field (Barrera, 2008 and unpublished data). All borers were collected from bored fruits in the field by dissecting them. To prevent falling or thrown borers from being lost in plant containers, we fitted a small plastic skirt around each plant to deflect borers onto the ground arena of mesocosms (Figure 1). 24 h after placing borers in mesocosms we checked all coffee fruits for evidence of borer holes and counted the total number of CBB in fruits on plants and on the ground. Tracking fruit damage as a measure of pest suppression was preferred over measuring borer mortality, because it was sometimes difficult to assess when individual borers were dead and if the cause of death was due to ant attack or environmental exposure in mesocosms. This also allowed for a more direct assessment of the impact of this nonconsumptive effect on crop damage suppression. Additionally, we counted all CBB individuals that were found outside fruits at the end of trials to track CBB movement and ensure that few borers were escaping the mesocosms (Appendix S1: Figure S1). To minimize the impact of residual ant pheromones or plant volatile chemicals, all plastic tubs were cleaned with alcohol in between trials. Coffee plants were alternated such that at least 48 h passed before being used again in experiments. To control for differences between mesocosms or coffee plants, treatments were assigned to each mesocosm randomly. In total, 59 trials were conducted ($N = 15$ control, $N = 13$ *Wasmannia* only, $N = 17$ *Azteca* only, $N = 14$ both ants) in blocks during the first 2 weeks of October 2016.

To assess whether the number of borers observed inside coffee fruits differed between treatments after 24 h we conducted GLMMs. We ran individual GLMMs on the number of borers in fruits on plants and the ground separately, and on the combined outcome. We included *Azteca* and *Wasmannia* presence or absence as fixed effects in the models. Their interaction was also included as a fixed effect to determine statistical significance of the both-ant treatment, which would indicate non-additive predator effects (for the combined data). Due to the heavily non-consumptive nature of the *Azteca*–CBB interaction (please refer to the section [Results](#)) we used additive models, as opposed to a multiplicative risk model (Sih et al., 1998), which is based on prey depletion effects through consumption (Mccoy et al., 2012). To account for count data, the models were run using a Poisson error distribution with a log link function. We corrected for observed overdispersion in our plant level model by running a Poisson-lognormal

error distribution using an observation-level random effect (Elston et al., 2001). In all models, mesocosm number and trial date (block) were added as random effects to account for any impacts of inconsistency in our laboratory environment. For all GLMMs, fixed effect parameters and the variance of random effects were estimated by maximum likelihood with Laplace approximation. All GLMMs were run using the “glmer” function from the *lme4* package, whereas GLMs were run using the “glm” function, both in R version 4.0.2 (R Core Team, 2021).

RESULTS

Does the nonconsumptive interaction vary across time or space with scale insect density?

Interestingly, in nearly 200 behavioral trials we observed only one occurrence of what appeared to be consumptive behavior by *Azteca* on the CBB. Overall, nearly 43% of cases resulted in the nonconsumptive effect of *Azteca* throwing or dropping borers from plants. Alternatively, borers were either not removed by *Azteca* or not found during the 3-min trials (this includes five cases in which borers fell or flew off plants on their own). Unexpectedly, we found no difference in the amount of adult scale on coffee branches between seasons (Figure 2 and Table 1), indicating that scale density available to *Azteca* did not vary across time. However, we did find a significant difference in the proportion of dropped borers by *Azteca* between the two sampling times (Figure 3 and Table 1), when more borers were thrown off plants during the dry season (removing the one case of consumption from the analysis). The proportion of borers that were thrown by *Azteca* was also positively influenced by the amount of scale that were present on individual coffee branches (Figure 4 and Table 1). Additionally, the results from our GLMM showed a significant interaction between branch scale and season on the nonconsumptive behavior, in which CBB throwing was more consistent across a range of scale densities during the dry season (Figure 4 and Table 1).

What is the impact of the nonconsumptive interaction on pest damage and multienemy interactions?

Overall, in the plant and ground combined data, we did not observe a difference in the number of borers found in fruits between our control treatments and treatments with *Azteca* only. However, we did observe a significant decrease in borers in the *Wasmannia* and both-ant treatments

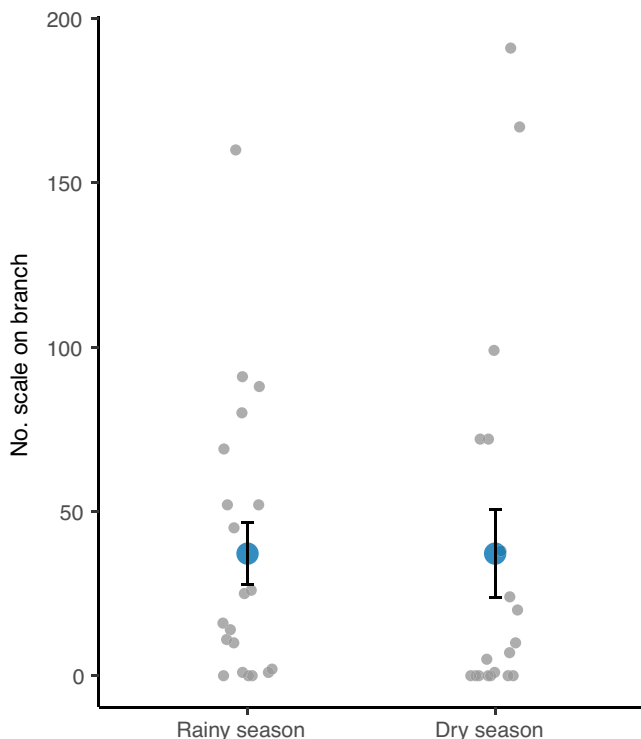


FIGURE 2 Number of adult scale insects on coffee branches by season. Raw data and means (\pm standard error) are shown (means shown in blue). Data from the rainy season were sampled in July 2019, whereas data from the dry season were sampled in February 2020. Data are pooled across several species of scale that are typically tended by *Azteca sericeasur* in this system.

(Appendix S1: Figure S2; Table 2). We did not find a significant interaction between *Azteca* and *Wasmannia* presence in our treatments, indicating that non-additive multipredator effects were not observed in the combined data set (Appendix S1: Figure S2; Table 2).

Separating plant and ground borer data, we observed opposite impacts of *Azteca* presence on borer infestation levels, which accounted for the lack of an effect for *Azteca* in the overall data. On the coffee plant, *Azteca* ants lowered the number of borers found in fruits by roughly 57% compared with controls (Figure 5a and Table 2), in line with previous evidence demonstrating the effectiveness of *Azteca* at reducing borer damage (Gonthier et al., 2013; Jiménez-Soto et al., 2013; Morris et al., 2015). However, because *Wasmannia* were restricted to the ground in this experiment, they had no effect on borer damage on the plant (Figure 5a and Table 2). The treatment with both ants also resulted in significantly fewer CBB in fruits on plants than in the control, reflecting the positive effect of *Azteca* ants on coffee plants (Figure 5a and Table 2).

On the ground, we observed a base level of damage in fruits in our control treatments from borers that had

TABLE 1 Summary of statistical model results for the field behavioral experiment.

Parameter	Estimate (\pm SE)	z-value	p ($> z $)
GLMM: proportion of CBB thrown ~			
Intercept	-1.544 \pm 0.452	-3.413	<0.001
Season	1.113 \pm 0.462	2.409	0.016
Scale	0.023 \pm 0.008	3.026	0.002
Season \times Scale	-0.017 \pm 0.009	-1.973	0.048
GLM: branch scale ~			
Intercept	3.615 \pm 0.037	98.537	<0.001
Season	<0.001 \pm 0.053	0.004	0.997

Notes: The generalized linear mixed model (GLMM) was run using a binomial error distribution (logit link). The generalized linear model (GLM) was run using a Poisson error distribution (log link). Parameter estimates (\pm SE), z-values, and p-values are provided. SE, standard error.

either fallen during trials on their own or flew off plants to the ground (Figure 5b and Table 2). *Wasmannia*-only ant treatments significantly reduced borer damage from these levels, however *Azteca*-only treatments significantly increased borer damage on the ground compared with the control (Figure 5b and Table 2), reflecting the non-consumptive throwing behavior of the ants. Although significantly less than the *Azteca*-only treatment, ground borer damage in the treatment with both ants was not different from the control (Figure 5b and Table 2).

DISCUSSION

Collectively, our results document a unique case study in natural pest control in which crop damage suppression is driven almost exclusively by the nonconsumptive attack of a dominant natural enemy. Our behavioral data show that the strength of this aggressive non-consumptive interaction—throwing CBBs off plants by *Azteca sericeasur*—may be driven by variability in alternative resources for *Azteca*, potentially resulting in variable pest control efficiency. Our multipredator laboratory experiment demonstrated how this nonconsumptive effect mediated spatial complementarity between arboreal and ground-foraging natural enemies and may result in enhanced reduction of borer damage, when ground foragers are present on farms.

Surprisingly, from our behavioral experiment, we show that this pest control interaction is almost exclusively non-consumptive, which is interesting considering the previously documented efficiency of *Azteca* in reducing borer damage on plants (Gonthier et al., 2013; Jiménez-Soto et al., 2013; Morris et al., 2015). Although we set out to test the hypothesis that this behavior may vary due to seasonal

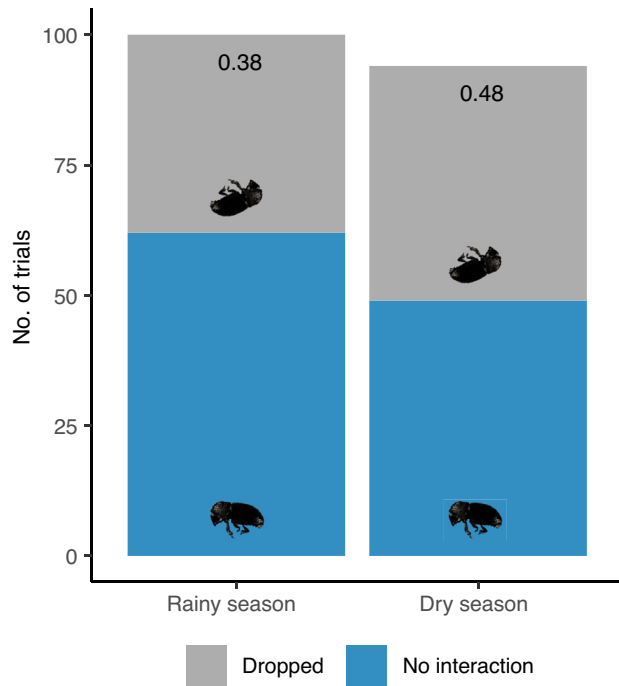


FIGURE 3 Number of coffee berry borers (CBB) thrown off plants by *Azteca sericeasur* by season. Total counts from behavioral trials are tallied for the different sampling times. Data from the rainy season were sampled in July 2019, whereas data from the dry season were sampled in February 2020. The overall proportion of CBB thrown by season is shown in bold at the top of columns.

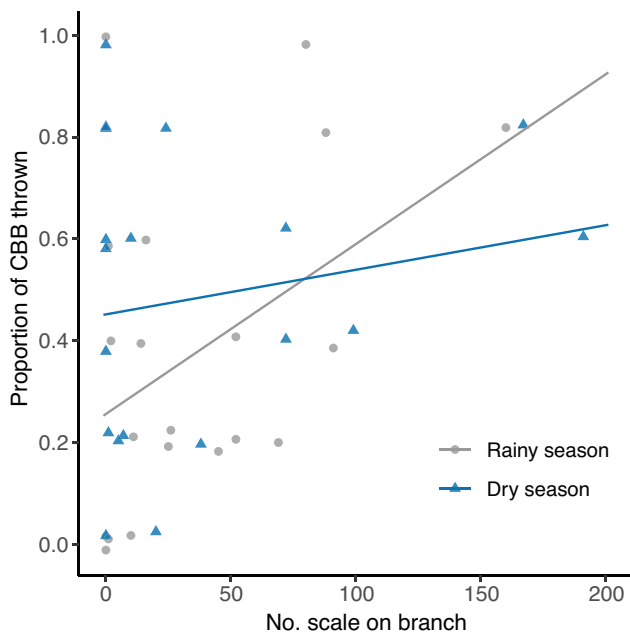


FIGURE 4 Proportion of coffee berry borers (CBB) thrown per plant across scale insect density. The relationship between the number of adult scale insects on coffee branches and the proportional result of *Azteca* behavioral trials for each coffee plant is shown. Proportions are calculated from the five behavioral trial replicates conducted per coffee plant. Trend lines show the relative effect of season by scale density.

TABLE 2 Summary of generalized linear mixed model results for the multipredator experiment

Parameter	Estimate (\pm SE)	z-value	p ($> z $)
Overall CBB damage~			
Intercept	2.944 \pm 0.063	46.477	<0.001
Azteca	-0.043 \pm 0.087	-0.495	0.620
Wasmannia	-0.316 \pm 0.099	-3.198	0.001
Azteca \times Wasmannia	-0.019 \pm 0.140	-0.136	0.891
Plant CBB damage~			
Intercept	2.182 \pm 0.177	12.327	<0.001
Azteca	-0.950 \pm 0.213	-4.456	<0.001
Wasmannia	0.045 \pm 0.217	0.207	0.836
Azteca \times Wasmannia	-0.025 \pm 0.322	-0.076	0.939
Ground CBB damage~			
Intercept	2.213 \pm 0.098	22.502	<0.001
Azteca	0.436 \pm 0.111	3.924	<0.001
Wasmannia	-0.779 \pm 0.167	-4.664	<0.001
Azteca \times Wasmannia	0.352 \pm 0.200	1.761	0.078

Notes: All models were run using Poisson error distributions (log link). Parameter estimates (\pm SE), z-values, and p-values are provided. The overall category shows the statistical results for the combined plant and ground CBB fruit damage. SE, standard error.

variation in resources from scale insects, we did not find a significant difference in scale abundance on coffee plants between seasons. However, we did still find a significant effect of season on borer throwing, in which slightly more borers were thrown during the dry season compared with the rainy season. We also found an overall significant positive effect of the density of scale insects on coffee branches on the frequency of *Azteca*'s throwing behavior, regardless of season, which aligns with related research showing a negative relationship between scale density and CBB damage on coffee with *Azteca* (Perfecto & Vandermeer, 2006; Rivera-Salinas et al., 2018). This suggests that the tendency for *Azteca* to exhibit this nonconsumptive behavior may be explained both by spatial variation in scale resources at different sites across coffee farms and by temporal variation across seasons.

Despite not finding a difference in scale abundance between seasons, it is possible that the effect of season on borer throwing that we observed was driven by the quality of honeydew resources from scale insects that may vary seasonally in the region of this study (Pringle et al., 2013). Research on ant-scale-plant interactions in Central America and Mexico has shown that water stress during dry seasons changes the concentration of carbohydrates within plants, which may cascade upward to affect scale honeydew quality and hemipteran-tending ant activity, ultimately impacting the ant defense of plants (Pringle et al., 2013). A previous study in our system used enclosure experiments on coffee bushes to show that *Azteca*'s

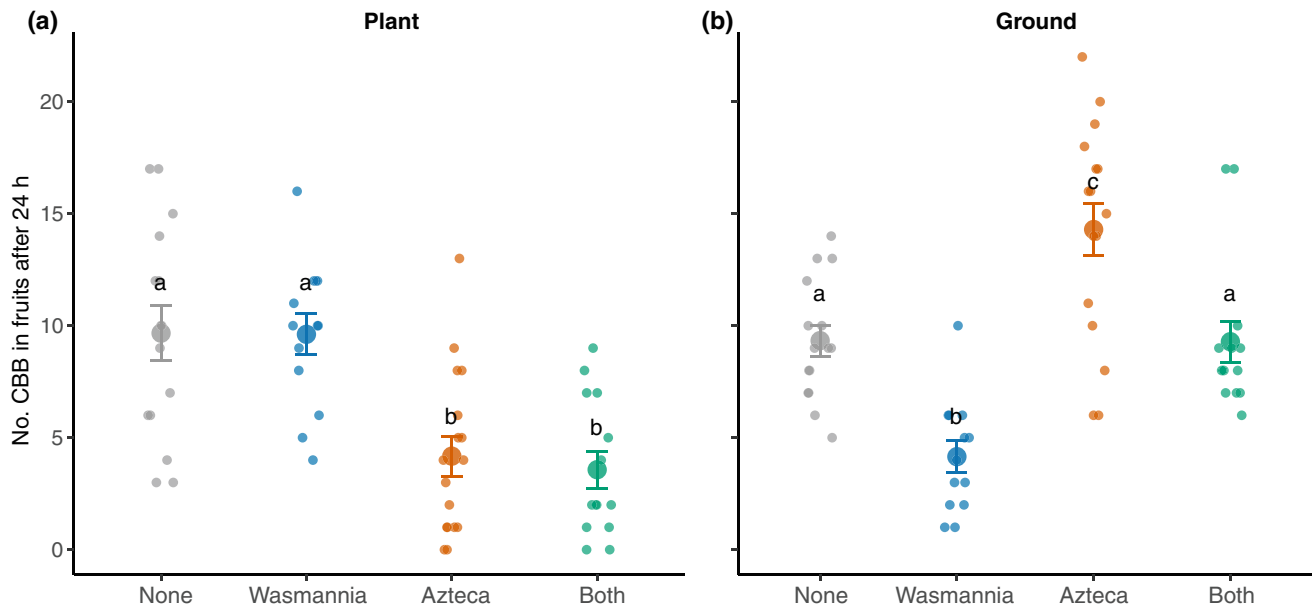


FIGURE 5 Number of coffee berry borers (CBB) in fruits on the plant and ground in mesocosms. The total number of CBB found bored into fruits on the plant (a) and the ground (b) at the end of the laboratory experiment after 24 h is shown. Raw data are shown for each treatment along with the mean (\pm standard error). Significant differences in means (from the generalized linear mixed models with Poisson error distribution and log link) for each figure are indicated with different letters.

suppression of borer damage also varied by time of year (Rivera-Salinas et al., 2018), which may be explained by variation in honeydew quality. Although we did not test honeydew composition in this experiment, our results aligned with the findings from Pringle et al. (2013) in that ant defense of plants is more consistent during the dry season than the wet season, potentially implying that seasonal differences in honeydew quality are at play. This would also explain the greater consistency in throwing we observed across a range of scale densities during the dry season. Additionally, variation in ant throwing behavior may be driven by seasonal differences in the nutritional needs of ant colonies across time (Cook et al., 2011). An important caveat is that, although we found these differences between two different sampling times with distinct precipitation levels, we were limited in our ability to infer long-term seasonal trends in nonconsumptive effects from these data. Regardless of the precise mechanism, nonconsumptive effects driven by predator aggression as opposed to prey behavior may result in distinct dynamics when driven by variation in alternate resources for enemies, which may ultimately result in variable or unreliable pest suppression. To our knowledge, this phenomenon has not been explored previously in natural pest control, and should be investigated further to understand the general impact of spatial and long-term seasonal (Hermann & Landis, 2017) variation in nonconsumptive enemy aggression on pest damage suppression.

In addition to our behavioral experiment, our multipredator experiment helped to illuminate some important

questions about the community ecology of this interaction. First, it appears that when there are no other predators in the system, many of the borers that are thrown off coffee plants by *Azteca* survive those attacks, potentially remaining in the borer population pool as reproductive individuals. Furthermore, thrown CBB individuals that survived attacks could relocate to old fruits on the ground or other coffee bushes and damage new fruits if *Azteca* is not foraging on those bushes. Despite the potential negative consequences of this “spillover” effect of thrown CBB, we also confirmed the results of previous laboratory (Pardee & Philpott, 2011; Philpott et al., 2012) and field experiments (Gonthier et al., 2013; Jiménez-Soto et al., 2013; Morris et al., 2015) that showed that *Azteca* is a highly efficient pest control agent in reducing borer damage on coffee bushes where they forage. Additionally, we demonstrated that a ground predator, *Wasmannia auropunctata*, suppressed borer individuals while foraging on the ground. Although it is already known that these ants, which nest both on plants and the ground, are important predators of borers on coffee plants (Gonthier et al., 2013; Newson et al., 2021), less research has focused on their potential to consume borers on the ground. This is despite their ability to enter borer holes where they potentially predate CBB larvae and pupae in old fruits that fall to the ground (Morris & Perfecto, 2016).

Regarding the impact of this nonconsumptive effect on multipredator interactions, the results from both experiments suggest that *Azteca* may significantly increase resource availability on the ground for ground-foraging

predators such as other ants, which could potentially result in facilitation or synergistic predator effects (Morris et al., 2018). However, despite this clear potential benefit for borer control, we did not find any evidence of non-additive effects from our multipredator experiment. Although *Wasmannia* presence consistently reduced borer damage, and in treatments with both ants more borers were made available to *Wasmannia* on the ground by *Azteca*, their rate of damage reduction did not appear to increase under these circumstances. In fact, *Wasmannia* ants reduced borer damage in fruits on the ground by roughly the same quantity in the both-ant treatment as in the *Wasmannia*-only treatment. One potential limitation is that we did not actually know from our data what quantity of borers were being directly consumed by *Wasmannia*, because we were only measuring the reduction in berry damage and not directly tracking ant behavior. However, we did observe parts of CBB individuals near *Wasmannia* containers in several replicates, and ants carrying CBB in their mandibles, suggesting that consumption did occur. Further research should investigate interactions between ants, ground-foraging predators, and herbivores under more realistic conditions in the field (Hermann & Landis, 2017) on mature coffee plants where predators can interact freely.

These contrasting results revealed the complexity of pest control interactions when nonconsumptive interactions are involved. Although there may be instances when *Azteca* ants do consume borers in the field, our data suggested that this occurred very infrequently, despite the well known importance of this ant for reducing borer damage. Interestingly, this behavior may actually explain the efficiency of *Azteca* as a keystone pest control agent. A previous field experiment conducted in this study system manipulated the densities of borers on coffee plants to which *Azteca* were exposed and found the same level of borer damage reduction across a range of pest densities (Morris et al., 2015). Importantly, this study failed to find a satiating effect at high densities of borers, which, given our results here, is probably explained by the fact that *Azteca* are simply not consuming CBB. This behavior may then ultimately result in the most efficient reduction of borers on coffee plants with high levels of *Azteca* activity. Subsequently, in farms with sufficient ground-foraging predator abundance, the “spillover” of these borer individuals from bushes with *Azteca* can be regulated by other predators, such as *Wasmannia*, reducing their survival and colonization of other coffee bushes. The both-ant treatment in our laboratory experiment resulted in the best overall control of CBB by first reducing borer damage on plants to its lowest levels and then minimizing the “spillover” from *Azteca*’s nonconsumptive effect of throwing borers to the ground, demonstrating the potential for

spatial complementarity between arboreal and ground-foraging natural enemies. Beyond ants, other predators, such as certain species of web-building spiders that form associative relationships with *A. sericeasur* in this region (Marín et al., 2015), may act as filters to collect resources thrown by *Azteca* and potentially buffer the effect of thrown borers and other pests. Additionally, thrown borers may also experience increased mortality risk from the loss of energy spent searching for refuges in old fruits on the ground, from potentially shifting their diets to these inferior resources, or from searching for new coffee plants to colonize.

Although nonconsumptive effects have long been studied in community ecology (Preisser et al., 2005; Schmitz et al., 2004; Werner & Peacor, 2003), there have been fewer examples of nonconsumptive mediated pest control (Hermann & Landis, 2017; Walzer & Schausberger, 2009). This study provides a unique addition to the existing literature, in which nonconsumptive natural enemy aggression, rather than prey defensive behavior (or direct predation), dominates pest damage suppression and drives spatial complementarity between natural enemies. Although this interaction may enhance coffee pest suppression in diverse communities when ground-foraging predators are conserved, variation in other resources that mediate *Azteca*’s aggressive behavior, such as scale insect abundance and potentially honeydew quality, could result in variable pest control efficacy. Future research exploring the impact of similar nonconsumptive interactions on pest populations (Sheriff et al., 2018) in diverse agroecological communities and under more realistic field conditions across growing seasons (Hermann & Landis, 2017) will help to illuminate the broader importance of these interactions for natural pest control. Ultimately, this case study demonstrates the complexity of natural pest control ecology and highlights the need to consider specific interaction mechanisms and spatial and temporal variability in those interactions for the management of this important ecosystem service (Vandermeer & Perfecto, 2017).

AUTHOR CONTRIBUTIONS

Jonathan R. Morris and Ivette Perfecto conceived of the project and experiments; Jonathan R. Morris designed experiments and collected data; Jonathan R. Morris analyzed the data; Jonathan R. Morris wrote the first draft of the manuscript; Jonathan R. Morris and Ivette Perfecto edited the manuscript together.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Morris, 2022) are available in Dryad at <https://doi.org/10.5061/dryad.hmgqnk9k0>.

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