



# Ecological complexity and contingency: Ants and lizards affect biological control of the coffee leaf miner in Puerto Rico

Ivette Perfecto<sup>a,\*</sup>, Zachary Hajian-Forooshani<sup>b</sup>, Alexa White<sup>b</sup>, John Vandermeer<sup>a,b</sup>

<sup>a</sup> School of Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, United States

<sup>b</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, United States

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## ABSTRACT

Complexity and contingency frame much of current thinking in population and community ecology. The coffee pest, *Leucoptera coffeella*, is particularly problematical in Puerto Rico, but is usually held under control in Mexico. A variety of arboreal ants are effective predators in Mexico, but are limited in an indirect fashion by the common aggressive arboreal ant, *Azteca sericeasur*. In Puerto Rico this species does not occur, suggesting that the small arboreal ants might be more effective predators there than in Mexico. However, the contingency of large population densities of Anoline lizards is well-known as a major biological control force for the leaf miner. Ants, especially the non-native *Wasmannia auropunctata*, have a negative effect on the lizards. Surveying ants and coffee leaf miners in 25 coffee farms in Puerto Rico, we investigate the effect of ants, in particular *W. auropunctata*, on the coffee leaf miner, and find that this ant species has a positive relationship with the miner. In a more detailed spatial study of two farms, surveys of anoline lizards show no significant negative relationship between the lizards and *W. auropunctata* on a per plant basis. However, we found a significantly lower abundance of lizards on patches dominated by this ant, suggesting that *W. auropunctata* indirectly protects the coffee leaf miner against this potential lizard predator. Thus, the structural complexity of a trait-mediated indirect effect occurs both in Mexico and Puerto Rico and potentially limits the effectiveness of biological control elements, but the contingencies are distinct in the two sites.

## 1. Introduction

Part of the general ecological narrative of complexity and contingency is the question of how various species interact in direct and indirect ways (the complexity) and how the outcome of those interactions changes depending on the species present or other circumstances (the contingency). Studies in Mexico provide evidence that the coffee leaf miner (*Leucoptera coffeella*) is partially controlled by a variety of ants, especially small twig nesting ants, common in coffee production systems (De la Mora et al., 2008; Lomeli-Flores et al., 2009). A major ant predator well-known in our study site in southern Mexico, *Azteca sericeasur*, was not effective as a controlling agent, a somewhat surprising result considering the aggressiveness of that particular species, and its complicity in control of other pests, especially the coffee berry borer (*Hypothenemus hampei*; Perfecto and Vandermeer 2006; Jiménez-Soto et al., 2013; Morris et al., 2015; Morris et al., 2017). Yet the relatively innocuous nature of the leaf miner at this Mexico site is notable. De la Mora and colleagues (2008) report that percentages of leaves with

mines range from 0 to 15 %, with most of them having zero damage, and even when attacked, the number and size of mines per leaf are usually small (personal observations). Lomeli-Flores and colleagues (2009) consider it to be a secondary pest in Mexico because it is of concern only in occasional years and on specific farms. Correspondingly, conversations with farmers in Mexico rarely include the leaf miner as a major source of concern. It has been suggested that the coffee leaf miner becomes a problem in sites where natural enemies are reduced due to regular pesticide applications and where coffee is cultivated under full sun conditions (i.e. low vegetational diversity) (Guharay et al., 2001; Fragoso et al., 2002).

The situation in Puerto Rico is substantially different from that in Mexico. Conversations with farmers routinely include the leaf miner as a, if not the, major pest problem in coffee. Indeed, in a sample of almost 2000 leaves at 25 farms dispersed across the coffee-growing region of Puerto Rico (Fig. 1) we find that 88 % of the farms had greater damage than the largest encountered in Mexico, and the average percent of number of leaves with mines was 66%. Given that some of the small

\* Corresponding author at: 440 Church Street, School for Environment and Sustainability, Dana Building, University of Michigan, Ann Arbor, MI 48109, United States.

E-mail address: [perfecto@umich.edu](mailto:perfecto@umich.edu) (I. Perfecto).

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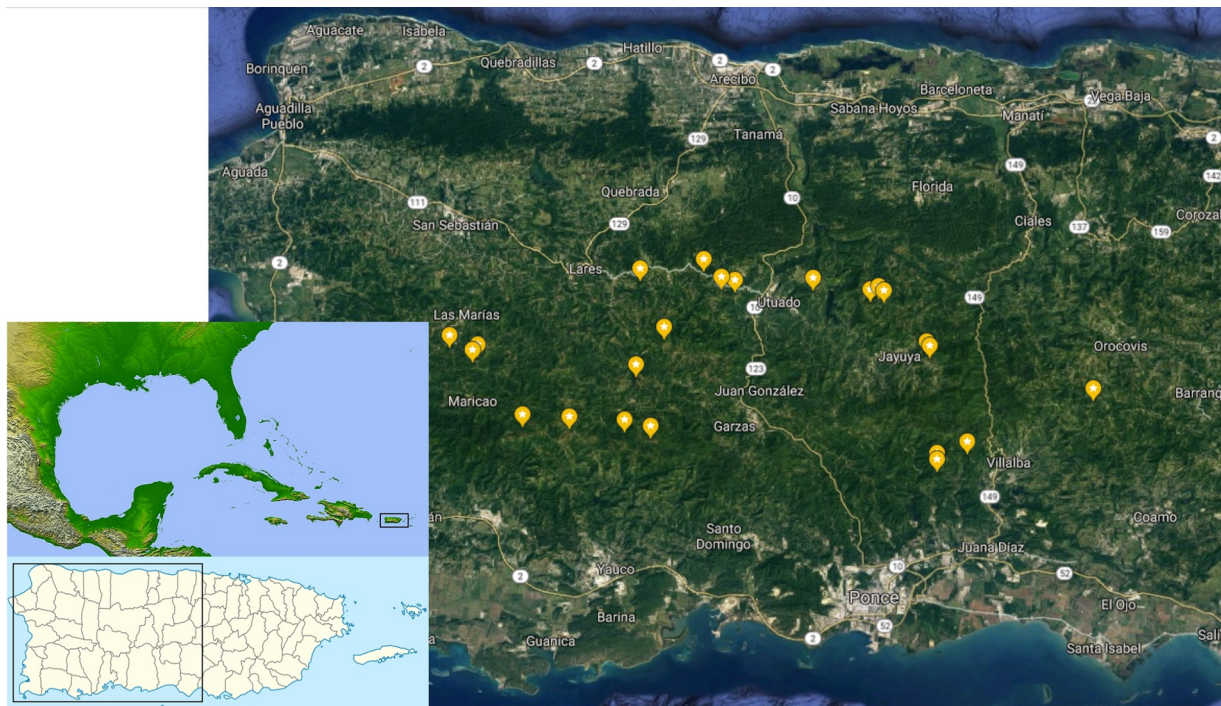


Fig. 1. Location of all 24 farms studied, encompassing most of the central coffee-producing area of the country.

ants are as common in Puerto Rico as in Mexico, that the small predaceous ants seem to be effective predators on the leaf miner in Mexico, potentially predators on eggs, larvae, and pupae (Lomeli-Flores et al., 2009), and the extensive literature on ants as predators on leaf miners in general (Faeth, 1980; Heads and Lawton, 1985; Hespeneheide, 1991; Pezzolesi and Hager, 1994), it is somewhat surprising that the situation in Puerto Rico should be so different from Mexico.

One of the main differences between Mexico and Puerto Rico regarding potential predators of the leaf miner is the high abundance of anoline lizards in Puerto Rico. Arboreal lizards in the genus *Anolis* are important insectivores in the Neotropics and reach the highest population densities of any lizards in the world (Schoener and Schoener, 1980; Vitt et al., 2003). In a comparative study between coffee farms in Mexico and Puerto Rico, Monahan and colleagues (2017) reported an estimate 43 lizards per hectare in Mexico versus 610 in Puerto Rico. In particular, throughout the Caribbean, anoline lizards drive the top-down regulation of arthropod communities (Spiller and Schoener, 1990). In an exclusion experiment in shade coffee farms in Puerto Rico, Borkhataria and colleagues (2006) reported a negative impact of anoles on selective herbivore pests. Although the effect on the leaf miner was complicated and highly variable, the final count showed a significantly higher abundance of mines in the lizard exclusion treatment as compared to the control. All of this suggests that anoles are important predators of the coffee leaf miner in Puerto Rico.

An obvious question emerges from this natural history. If the lizards are effective natural enemies of the coffee leaf miners and there are so many of them within coffee farms, why are the infestation rates of the leaf miners so high in Puerto Rico? We approach this question by examining interactions between the ants and the lizards and their effect on the leaf miners. In a previous study we reported a negative interaction between *Wasmannia auropunctata* and anoline lizards in coffee farms in Puerto Rico (Perfecto et al., 2019). Here, we propose that the “contingency” of a principle controlling agent of the adult coffee leaf miner is the presence of large number of predaceous lizards in Puerto Rico, compared to Mexico. The “complexity” arises from the indirect effect the ants seem to have on those lizards. In other words, the most abundant natural enemy in Puerto Rico may be deterred by the non-native *Wasmannia auropunctata*, resulting in the high incidence of this

pest in Puerto Rican coffee farms as compared to Mexico.

## 2. Methods

From a data base of 85 farms, vegetative, productive, and management characteristics were evaluated during the summer of 2018 (Perfecto et al., in review). From this data base, 25 farms thought to represent the range of possible conditions, both in terms of spanning the range of coffee producing regions and the management styles, were chosen for more detailed analysis, especially for the major pests of coffee (Fig. 1). Leaf miner activity was one of the variables measured. Management style of farms ranged from coffee monocultures (sun coffee) to forest-like shaded coffee, with the majority of the farms intermediate with coffee intercropped with a variety of fruit trees (mainly citrus), plantains/bananas and some root crops. With the exception of one farm, all farms received sporadic pesticide applications, including the herbicide glyphosate and two systemic insecticides, disulfoton (DySyston) and aldicarb (Temik). Location and elevation for all 25 farms can be found in the supplementary materials Table S1.

At monthly intervals, we sampled leaf miners at each of the 25 sites. Sampling period spanned from September to December, 2018. Within a permanent 10 x 10 m plot chosen with the intent of representing the basic management style of the overall farm, 20 randomly selected plants were marked and measured each sampling period. Stratifying the sampling, an arbitrary branch from top, middle and bottom levels on the bush were chosen and the number of mines on each leaf on the branch were recorded, along with an estimate of the total number of leaves per plant. For the present study, the percentage of leaves with miners per coffee plant was analyzed.

During the period from Dec 2018 and Jan 2019, all 20 coffee plants within the 10 x 10 m plot at each of the 25 farms, were surveyed with tuna fish baits, for ant activity. Baits consisted of a teaspoon of tuna fish in oil placed on the trunk of coffee plants. Five baits were placed at various heights going from the lower branches to the higher branches on each coffee plant and allowed to set for 40 min., after which the presence and species of ants on each bait and within 10 cm of the bait was recorded (Romero and Jaffe, 1989; Ellison et al., 2007). Activity was defined as the number of baits occupied by a particular ant species.

Since most of the ants are members of common species we were mainly able to identify them on sight. However, when an unknown species was encountered we collected a sample and brought it to the laboratory for further identification. These samples were identified using a combination of Bolton's *Catalogue of Ants of the World* (Bolton et al., 2006), *Puerto Rico AntWiki*, and the unpublished version of *The Ants of Puerto Rico* (Hymenoptera: Formicidae) by Roy Snelling and Juan Torres.

Within logistical and accessibility criteria, two farms were chosen for yet more detailed study, the farm coded UTUA2 (Grand Batey) (lat = 18.287858; long = -66.770264) and the farm coded UTUA20 (Raul Toledo) (lat = 18.27949 ; long = -66.828209), both in the municipality of Utuado. In an area of approximately 0.5 ha. all coffee plants were surveyed with tuna fish baits, for ant activity, as described above. At a later point in time subsamples of plants were examined for mines from *L. coffeella* (using the same protocol as on the rest of the farms). Forty coffee plants within the area denoted Area I, and 40 plants within the area denoted Area II (Fig. 3) were sampled on farm UTUA2. On farm UTUA20 a total of 40 plants, 10 from each of the areas dominated by one of the three dominant ant species and 10 from the area with low ant abundance were sampled. To assess the abundance of anoline lizards, individual coffee trees were carefully approached from two sides by two independent observers, and the total number of individual lizards observed on a tree within a two min. period was recorded, in areas with low ant abundance (area II in UTUA2 and area I in UTUA20) and areas with high ant abundance (area I in UTUA2 and areas IIa and b, and III in UTUA20; see Figs. 3 and 4). Lizard observations were conducted from 8:00 am to 11:00 am.

Statistical methods include standard linear regression analysis and computation of significance probability and  $R^2$  values. For the detailed study of the two farms (UTUA2 and UTUA20) leaf miner data was compared between plants with and without ants and with and without lizard using a direct bootstrapping test – using 10,000 samples of combined data, artificial partitions of the same sampling numbers as in the real samples were randomly constructed. The proportion of differences between the two sample means that are larger than the observed number is taken as the significance probability. With this method, no assumptions need to be met. Code for bootstrapping was written in MATLAB®.

### 3. Results

A total of 18 species of ants belonging to 11 genera were found (Table 1; for complete data see Table S2 in supplementary materials), although the vast majority (84%) were in five principal species (*Wasmannia auropunctata*, *Solenopsis invicta*, *Monomorium floricola*, and

*Tapinoma melanocephalum*), all potential predators on eggs, larvae, and pupae of the miner (De la Mora et al., 2008; Lomeli-Flores et al., 2009), and none reported to be native to the island (Torres and Snelling, 1997). Basically, there appear to be five distinct “ant community types” 1) dominated by *W. auropunctata*, 2) dominated by *S. invicta*, 3) dominated by *M. floricola*, 4) dominated by *T. melanocephalum*, and 5) co-dominated by *T. melanocephalum* and *M. floricola*. In Table 2 we summarize some of the characteristics of the ant species on each of the sampled farms.

Plotting the total ant abundance per site against the average percent coffee leaf miner damage at each site, we obtain a non-significant result (Fig. 2a). However, it is evident from Fig. 2a and Table 2 that we have two distinct classes of farms with regard to total ant density, high-density farms and low-density farms. Considering the high-density farms only (above 80% of all baits occupied by some species of ant), we obtain the results shown in Fig. 2b. There is a strong positive relationship between ant activity and fraction of leaves with miners, but it is the opposite of what was expected under the hypothesis that ants are controlling the leaf miner. One of the major species contributing to the high ant activity is the highly invasive electric fire ant, *Wasmannia auropunctata*, the effect of which can be statistically discerned for those farms with a sufficiently large number of them, again, in a positive direction (Fig. 2c). Indeed, it would seem that for those farms with high ant activity, the ants have a negative “ecosystem service,” or an “ecosystem disservice,” in that they promote more leaf miners, a pattern that calls for an explanation and is contrary to what others have reported (De la Mora et al., 2008; Lomeli-Flores et al., 2009).

The general result, then, is that at the local level (at the level of an individual coffee plant) there is no relationship between ant activity (whatever species or group of species is considered), but at a larger regional level, a strong effect of ants can be discerned, but in the opposite direction of what would be expected if ants were providing a biological control service.

An explanation that has been suggested (Perfecto et al., 2019) is that the abundant anoline lizards (genus *Anolis*) across the whole island, and especially on coffee farms, are potential predators on the coffee leaf miner adults (Borkhataria et al., 2006; Iverson et al., 2019). The ant, *W. auropunctata*, has been shown to have a negative effect on the presence of lizards, at a regional level, even if at the local level (the plant level) the pattern is not so clear (Perfecto et al., 2019).

In a survey of arboreal ants on all coffee plants on more extensive areas of two of the farms in our sample (UTUA2 and UTUA20) we encountered clustered patterns of the two most dominant ant species, *Solenopsis invicta* and *Wasmannia auropunctata* (Figs. 3 and 4). Sampling the number of mines on particular plants with and without the

**Table 1**

List of the ant species encountered in baiting on each of 25 farms with 100 baits set on 20 coffee bushes on each farm.

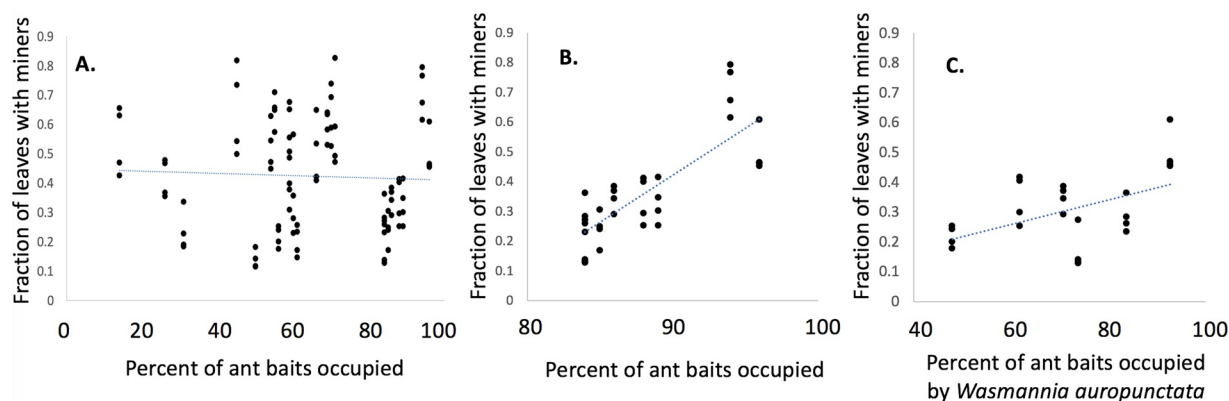
Species	Common Names	Number of Farms Occurrence	Number of Farms Dominant	Percent of Total Baits Occupied
<i>Solenopsis invicta</i>	Red imported fire ant	18	7	22.22
<i>Wasmannia auropunctata</i>	Electric ant or Little fire ant	16	10	36.77
<i>Monomorium floricola</i>		15	3.5	15.45
<i>Tapinoma melanocephalum</i>	Ghost ant	13	2.5	9.85
<i>Brachymyrmex heeri</i>		12	0	2.19
<i>Brachymyrmex obscurior</i>		7	0	1.93
<i>Nylanderia pubens</i>	Tawny crazy ant	6	0	1.67
<i>Pheidole megacephala</i>	African big-headed ant	5	0	2.38
<i>Monomorium ebenium</i>		4	0	2.45
<i>Linepithema iniquum</i>		3	0	2.70
<i>Myrmelachista ramulorum</i>		2	0	0.84
<i>Paratrachina longicornis</i>	Longhorn crazy ant	2	0	0.19
<i>Solenopsis globularia</i>		2	0	0.13
<i>Cardiocondyla emeryi</i>		1	0	0.06
<i>Pheidole moerens</i>		1	0	0.77
<i>Solenopsis pollux</i>		1	0	0.26
<i>Cardiocondyla venustula</i>		1	0	0.06
<i>Pheidole sculptor</i>		1	0	0.06



**Table 2**

Summary of the 25 farms in the study and the activity patterns of the five most common species (see Table 1 for complete scientific names).

FARM CODE	W.a.	S.i.	M.f.	T.m.	TOTAL ACTIVITY	NUMBER OF DOMINANT SPECIES	COMMUNITY CATEGORY
ADJU7	0	0	47	3	50	1	M.f.
ADJU8	0	65	20	0	85	2	S.i.
JAYU2	0	12	3	3	18	3	S.i.
JAYU3	0	4	19	31	54	3	M.f./T.m.
JUAN1	23	1	2	12	38	4	W.a.
JUAN7	0	20	24	8	52	3	S.i./M.f.
LASM1	62	24	0	0	86	2	W.a.
LASM2	3	15	0	0	18	2	S.i.
LASM3	84	0	0	0	84	1	W.a.
MARI2	71	3	0	11	85	3	W.a.
MARI3	39	2	0	17	58	3	W.a.
MARI8	48	0	0	0	48	1	W.a.
OROC1	13	0	0	0	13	1	W.a.
PONC1	40	21	6	0	67	3	W.a.
UTUA10	1	2	17	22	42	4	M.f./T.m.
UTUA13	0	39	6	1	46	3	S.i.
UTUA16	93	0	0	0	93	1	W.a.
UTUA17	1	14	6	26	47	4	T.m.
UTUA18	4	5	44	0	53	3	M.f.
UTUA2	74	0	2	0	76	2	W.a.
UTUA20	7	38	2	5	52	4	S.i.
UTUA30	0	3	41	12	56	3	M.f.
UTUA5	8	48	1	2	59	4	S.i.
YAUC3	0	29	0	0	29	1	S.i.
YAUC5	0	0	0	0	0	0	NA
SUM	571	345	240	153	1309		



**Fig. 2.** A. All four sampling dates at all 24 farms, illustrating a general non-significant trend. B. Consideration of only the eight “ant-dense” farms, a significant relationship is found ( $p < 0.0001$ ;  $R^2 = 0.64$ ), but in the opposite direction of expectation. C. Only farms with 40 or more baits occupied by *W. auropunctata*, the relationship with this species alone is significant ( $p = 0.0116$ ;  $R^2 = 0.25$ ).

dominant ant species, it was found that the average percentage of leaves attacked by miners was greater on plants with high ant activity than on plants with low ant activity ( $p < 0.05$ , by a bootstrapping test at both sites; Fig. 5). Sampling the number of anoline lizards on 80 coffee plants in the same two areas of the UTUA2 site (40 coffee plants within the area denoted Area I, and 40 plants within the area denoted Area II; Fig. 3) we found no relationship between the presence of *W. auropunctata* and the presence of anoles on a per plant basis (either in area I or II separately, or the two areas combined). However, there was a significant difference when comparing overall anole abundance between Area I and Area II, with the first having an average of 0.84 anoles per plant, while the second had an average of 1.4 anoles per plant ( $p < 0.05$ , by the bootstrapped test; Fig. 5). Similarly, at the UTUA20 site, sampling 10 plants in each of the three ant categories (Fig. 4), we found no relationship between the presence of any of the two dominant ant species and the presence of anoles on a per plant basis. However, there was a significant difference when comparing overall anole abundance between the areas I (no aggressive ants present) and the combination of II and III (presence of *W. auropunctata* or *S. invicta*; Fig. 4).

This result conforms to the more regional result that farms with more ants generally had more miners, at least for the farms with higher ant activity (Figs. 2b and c), of which UTUA2 and UTUA20 are examples.

#### 4. Discussion

In this study we show that the particular species that are present in a community, along with the indirect interactions that result from those particular species, can produce very different situations regarding the outcome of pest control by natural enemies. In Mexico, the ant community appears to play a major role controlling the coffee leaf miner (De la Mora et al., 2008; Lomeli-Flores et al., 2009). However, in Puerto Rico, the high density of ants, especially *W. auropunctata*, in some patches, interact negatively with the anoline lizards, and interfere with their predatory activity, resulting in higher incidence of the leaf miner when the ants are present at high densities. In the Mexico case, there is direct evidence that small predacious twig nesting ants are effective predators (De la Mora et al., 2008), yet the indirect interference of those ants by the aggressive dominant *A. sericeus* reduces the efficiency of

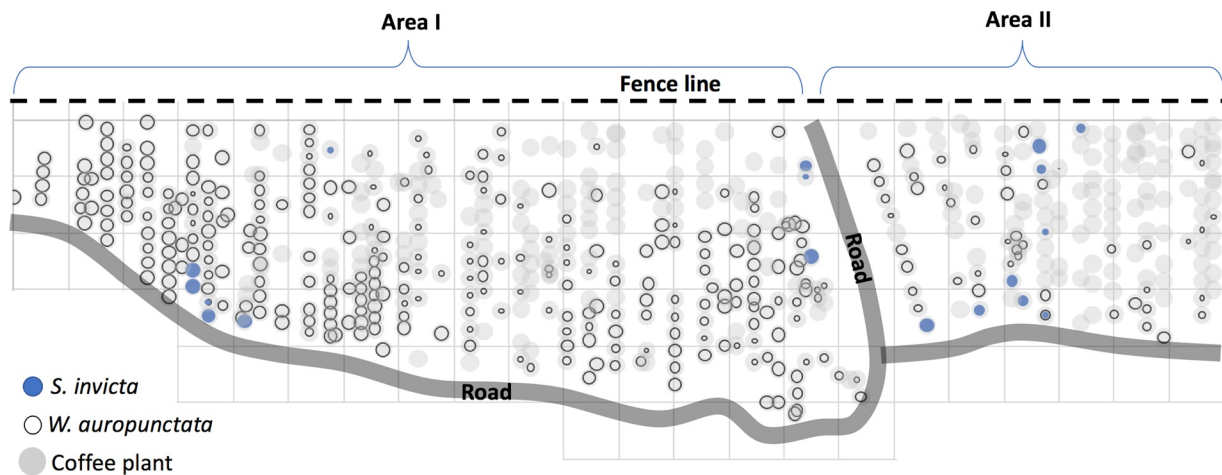


Fig. 3. Detailed map of the UTUA2 farm for two of the major arboreal ant species (*Wasmannia auropunctata* = open circles; *Solenopsis invicta*, closed blue circles). Size of bubble proportional to ant activity (0 – 5), based on the number of tuna fish baits occupied after 40 min. Each bubble is in the position of an individual coffee plant for a total of 547 coffee plants. Area I and Area II are the zones where Anole and leaf miner sampling was employed.

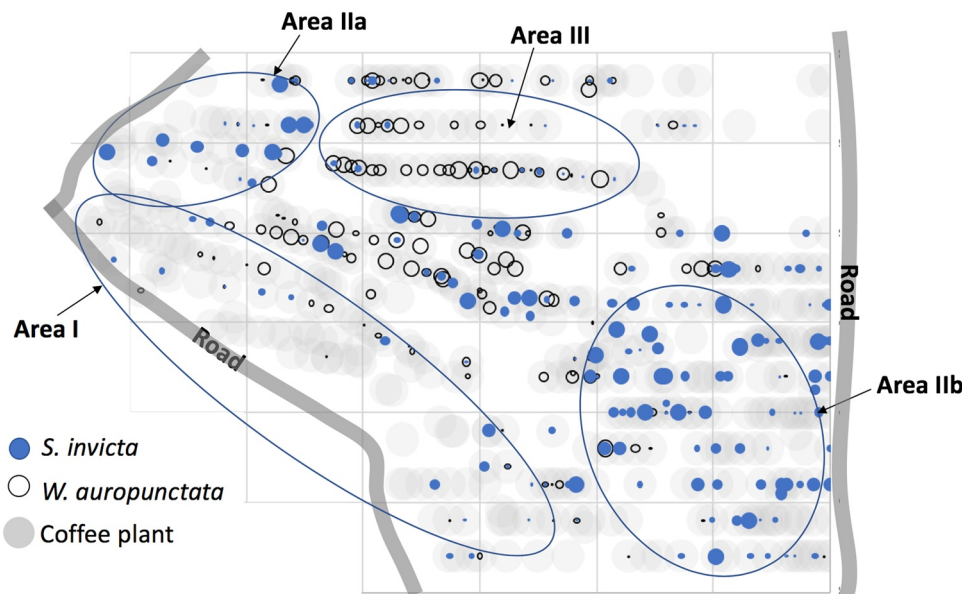


Fig. 4. Detailed map of the UTUA20 farm for three of the major arboreal ant species (*Wasmannia auropunctata* = open circles; *Solenopsis invicta* = blue). Size of bubble proportional to ant activity (0 – 5), based on the number of tuna fish baits occupied after 40 min. Each bubble is in the position of an individual coffee plant for a total of 496 coffee plants. Sampling areas indicated with ovals corresponding to regions dominated by particular species.

these other arboreal ants to some extent, but not enough to make the coffee leaf miner a significant pest (Philpott, 2010; Philpott et al., 2008, 2012). Although direct evidence is lacking, there is no reason to suggest that the sorts of small arboreal ants common in coffee in Puerto Rico would not prey on the immature forms of the miner, as they do in other systems (Faeth, 1980; Heads and Lawton, 1985; Hespeneide, 1991; Pezolesi and Hager, 1994). Furthermore, based on reports of ants as major predators of the coffee leaf miner (De la Mora et al., 2008; Lomeli-Flores et al., 2009), we expected a negative relationship between ant activity on a plant and the percent leaf miner incidence on that plant, an expectation that is qualitatively true (i.e. a negative regression coefficient), but far from statistically significant, even with a large sample size (480 plants sampled –  $R^2$  for a simple linear regression = 0.009; Fig. 2a). However, if we ask about the community assemblage characteristics of each farm, an interesting, and counterintuitive result emerges – leaf miner attack is positively related to ant activity within a patch (Fig. 2b and c), even though it does not reveal itself at a local (coffee plant) level.

The situation in Puerto Rico appears to be related to the predacious activities of the abundant anoline lizards that occur at very high densities on all coffee farms in the country. Through lizard exclusion

experiments, Borkhataria et al. (2006) demonstrated that anoles have a negative effect on the coffee leaf miner. Here and elsewhere (Perfecto et al., 2019) we present evidence that lizards avoid areas where dominant and potentially aggressive ants, especially *W. auropunctata*, are abundant. Thus, ants, which are potentially important predators of the various life stages of the leaf miner, play an overall negative role in acting to scare away lizards. It is a classic trait-mediated indirect interaction, wherein a potential biological control agent is indirectly excluded from relatively large areas by another, presumably less efficient, control agent (Snyder and Ives, 2001; Schmitz et al., 2004; Chailleux et al., 2014). The parallels and distinctions between Mexico and Puerto Rico cases are diagrammatically illustrated in Fig. 6.

Much of this is, in retrospect, understandable. Larval leaf miner behavior exposes the organism to attack by any predator nearby, an especially likely event with such a visual predator as anoline lizards (Steinberg and Leal, 2016). For example, in Fig. 7 we display 0.5 sec frames of a larvae in the act of spinning its cocoon. It is evident that the back and forth movement that is required of the larvae to spin its cocoon makes it especially vulnerable to visual predators. Field observations suggest that after 15 minutes of spinning, a visible silk covering can be seen, but only covering the posterior part of the body. After 50

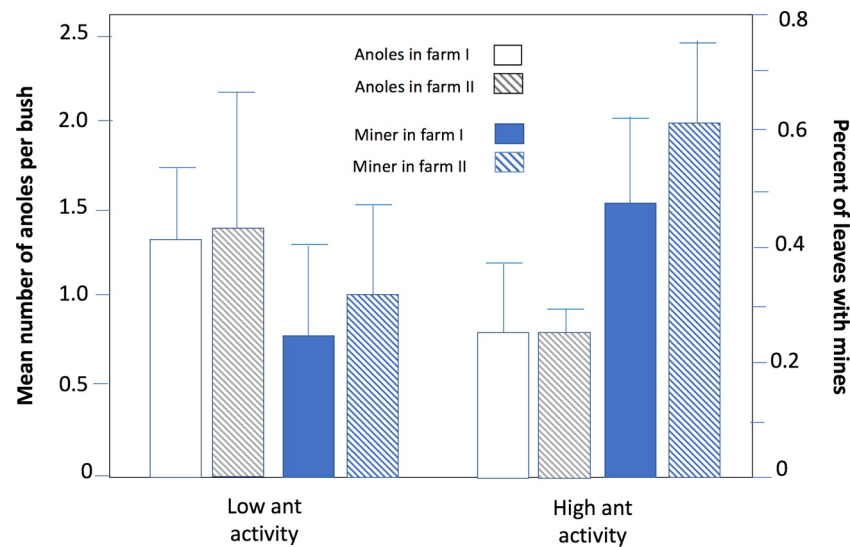


Fig. 5. Average percentage of leaves with coffee leaf miner damage, and average number of anoline lizards on coffee plants within an area with high ant activity versus an area with low ant activity in farm UTUA2 (farm I) and UTUA20 (farm II).

minutes, the anterior part of the body is still spinning back and forth and would seem an attractive bait for a visual predator. It takes approximately one to one and a half hours before the larvae appears to be completely protected within its cocoon. This would seem to be an especially vulnerable interval for predation pressure, from either ants or, especially, lizards and other vertebrate predators. Anoline lizards could be effective predators of the adult stage of the coffee leaf miner, although this has not been evaluated. Although adults tend to be nocturnal and crepuscular, they spend their time on coffee plants and have been observed mating in the mornings after the dew dries, and when the lizards are active (Walker and Quintana, 1969; Guerreiro Filho, 2006).

From a practical point of view, the species of ant with seemingly the biggest effect, *W. auropunctata*, is regarded by many farmers as one of the most noxious pests in the system because of the painful sting it inflicts on people harvesting the coffee (Wetterer and Porter, 2003). At harvest time various hemipterans tend to concentrate near clusters of fruits, and *W. auropunctata* individuals tend to aggregate around them to feed on their honeydew. That is precisely where the workers tend to pick up individuals who then travel unfelt to softer tissues of the body and present the workers with a rather painful sting. In Puerto Rico, farmers have reported to us that workers frequently pass by areas that have high concentrations of *W. auropunctata* ants, thus indirectly reducing the productivity of those parts of the farm.

On the other hand, this species has also been found to be a predator of another main pests of coffee, the coffee berry borer (Vazquez Moreno et al., 2006; Armbricht and Gallego, 2007; Tribble and Carroll, 2014; Morris and Perfecto, 2016). This highlights the importance of understanding the ant community and the impacts of the different species on potential pests in agroecosystems. Rather than applying an insecticide to get rid of *W. auropunctata* (which is what some farmers do) to encourage higher predation of anoles on the coffee leaf miner, it may be better to manipulate the ant community to reduce *W. auropunctata* activity during the periods of high densities of the leaf miners, but letting it to flourish during periods when the coffee berries are maturing and are susceptible to colonization by the coffee berry borer.

## 5. Conclusion

Both Mexico and Puerto Rico exhibit a characteristic indirect trait-mediated effect on the control of the coffee leaf miner. In Mexico the keystone dominant ant *A. sericeus* acts to reduce the foraging efficiency of the smaller twig-nesting ants that are reported to be predators of the leaf miner eggs, larvae and adults, however, this interference does not seem to be enough to make the coffee leaf miner a major pest in coffee in this region (Lomeli-Flores et al., 2009). It is likely that this species also acts to deter adults from laying eggs in the first place, due to its basic behavior of intimidating anything that may be predacious on

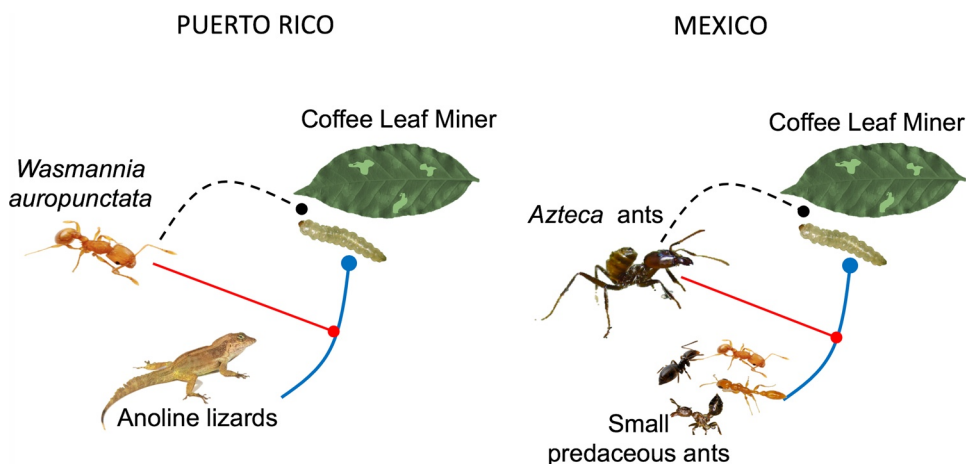


Fig. 6. Diagrammatic view of the difference between Puerto Rico and Mexico in terms of the distinct contingent elements (*Wasmannia* versus *Azteca* ants and anole lizards versus smaller predacious ants) but the similar dynamic connections with a trait-mediated effect. Small circles at the ends of each line indicate a negative effect. A trait-mediated indirect effect is illustrated by the red line that connects one of the connectors. The dashed black line indicates the indirect interaction.



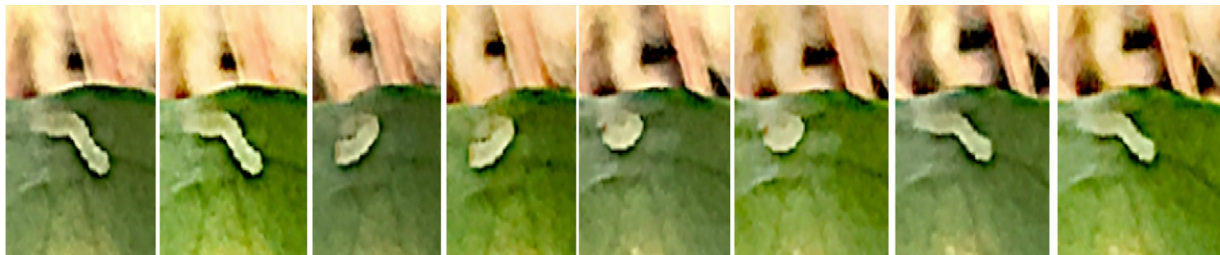


Fig. 7. Eight frames, separated by about 0.5 seconds each, illustrating the back and forth movement of the larvae as it weaves its pupal case.

the Hemipterans it tends (Vandermeer et al., 2010). Puerto Rico presents a very distinct set of contingencies, but with a similar trait-mediated dynamic operative, in which a seemingly efficient predator, anole lizards, are dissuaded from occupying areas with high ant activity, especially the common *W. auropunctata*, as diagrammed in Fig. 6. *Wasmannia auropunctata* was been reported as a major pest in some agricultural systems, including coffee farms, because it has a painful sting and dissuade coffee pickers from harvesting coffee in areas with high densities of this species. This study presents evidence that *W. auropunctata* can also have negative impacts on coffee by interfering with the predation of the coffee leaf miner by the abundant anoline lizards on the island. Since *W. auropunctata* has also been reported to be a predator of the coffee berry borer, another main coffee pest in Puerto Rico and worldwide, strategies should be developed to manipulate the ant community in order to reduce *W. auropunctata* activity at times when the leaf miner represents a problem, while maintaining it at times when the coffee is susceptible to berry borer attack. This is not an easy task to achieve but one that would only be possible if we understand the ecology of the agroecosystem.

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## Declaration of Competing Interest

The authors reported no declarations of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107104>.

## References

- Armbricht, I., Gallego, M.C., 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomol. Exp. Appl.* 124 (3), 261–267. <https://doi.org/10.1111/j.1570-7458.2007.00574.x>.
- Borkhataria, R.R., Collazo, J.A., Groom, M.J., 2006. Additive effects of vertebrate

- predators on insects in a Puerto Rican coffee plantation. *Ecol. Appl.* 16, 696–703. [https://doi.org/10.1890/1051-0761\(2006\)016\[0696:AEVPO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0696:AEVPO]2.0.CO;2).
- Chailleux, A., Mohl, E.K., Teixeira Alves, M., Messelink, G.J., Desneux, N., 2014. Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Mgmt. Sci.* 70, 1769–1779. <https://doi.org/10.1002/ps.3916>.
- De la Mora, A., Livingston, G., Philpott, S.M., 2008. Arboreal ant abundance and leaf-miner damage in coffee agroecosystems in Mexico. *Biotropica* 40, 742–746. <https://doi.org/10.1111/j.1744-7429.2008.00444.x>.
- Ellison, A.M., Record, S., Arguello, A., Gotelli, N.J., 2007. Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. *Environ. Entomol.* 36 (4), 766–775. <https://doi.org/10.1093/ee/36.4.766>.
- Faeth, S.H., 1980. Invertebrate predation of leaf-miners at low densities. *Ecol. Entomol.* 5, 111–114.
- Fragoso, D.B., Guedes, R.N.C., Picanço, M.C., Zambolim, L., 2002. Insecticide use and organophosphate resistance in the coffee leaf miner *Leucoptera coffeella* (Lepidoptera: Lyonetiidae). *B. Entomol. Res.* 92 (3), 203–212. <https://doi.org/10.1079/BER2002156>.
- Guharay, F., Monterroso, D., Staver, C., 2001. El diseño y manejo de la sombra para la supresión de plagas en cafetales de América Central. *Agroforestería en las Américas* 8 (29), 22–29.
- Heads, P.A., Lawton, J.H., 1985. Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecol. Entomol.* 10, 29–42.
- Hespenheide, H.A., 1991. Bionomics of leaf-mining insects. *Ann. Rev. Entomol.* 36, 535–560.
- Iverson, A.L., Gonthier, D.J., Pak, D., Ennis, K.K., Burnham, R.J., Perfecto, I., et al., 2019. A multifunctional approach for achieving simultaneous biodiversity conservation and farmer livelihood in coffee agroecosystems. *Biol. Conserv.* 238, 108179. <https://doi.org/10.1016/j.biocon.2019.07.024>.
- Jiménez-Soto, M.E., Cruz-Rodríguez, J.A., Vandermeer, J., Perfecto, I., 2013. *Hypothenemus hampei* (Coleoptera: Curculionidae) and its interactions with *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a shade coffee agroecosystem. *Environ. Entomol.* 42, 915–924. <https://doi.org/10.1603/EN12202>.
- Lomeli-Flores, J.R., Barrera, J.F., Bernal, J.S., 2009. Impact of natural enemies on coffee leaf miner *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) population dynamics in Chiapas, Mexico. *Biol. Control* 51 (1), 51–60. <https://doi.org/10.1016/j.biocontrol.2009.03.021>.
- Morris, J.R., Vandermeer, J., Perfecto, I., 2015. A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities. *PLoS One* 10 (11), e0142850. <https://doi.org/10.1371/journal.pone.0142850>.
- Morris, J.R., Perfecto, I., 2016. Testing the potential for ant predation of immature coffee berry borer (*Hypothenemus hampei*) life stages. *Agric. Ecosyst. Environ.* 233, 224–238. <https://doi.org/10.1016/j.agee.2016.09.018>.
- Perfecto, I., Hijian-Forooshani, Z., Iverson, A.D., Lugo Pérez, J., Medina, N., Vaidya, C., White, A., Vandermeer, J., 2019. Response of coffee farms to hurricane Maria: resistance and resilience from an extreme climatic event. *Sci. Rep.* 9 (1), 1–11.
- Perfecto, I., Vandermeer, J., 2006. The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. *Agric. Ecosyst. Environ.* 117 (2–3), 218–221. <https://doi.org/10.1016/j.agee.2006.04.007>.
- Pezzolesi, L.S.W., Hager, B.J., 1994. Ant predation on two species of birch leaf-mining sawflies. *Am. Midland Nat.* 156–168.
- Philpott, S.M., Perfecto, I., Vandermeer, J., 2008. Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. *J. Anim. Ecol.* 77, 505–511. <https://doi.org/10.1111/j.1365-2656.2008.01358.x>.
- Philpott, S.M., 2010. A canopy dominant ant affects twig-nesting ant assembly in coffee agroecosystems. *Oikos* 119, 1954–1960. <https://doi.org/10.1111/j.1600-0706.2010.18430.x>.
- Philpott, S.M., Pardee, G.L., Gonthier, D.J., 2012. Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity. *Ecology* 93, 992–1001. <https://doi.org/10.1890/11-1431.1>.
- Romero, H., Jaffe, K., 1989. A comparison of methods for sampling ants (Hymenoptera, Formicidae) in savannas. *Biotropica* 24 (4), 348–352.
- Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7, 153–163. <https://doi.org/10.1111/j.1461-0248.2003.00560.x>.
- Schoener, T.W., Schoener, A., 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *J. Anim. Ecol.* 49 (1), 19–53.
- Snyder, W.E., Ives, A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82, 705–716. [https://doi.org/10.1890/0012-9658\(2001\)082\[0705:GPDRBC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0705:GPDRBC]2.0.CO;2).

- 082[0705:GPDBCB]2.0.CO;2.
- Spiller, D.A., Schoener, T.W., 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature* 347 (6292), 469–472.
- Steinberg, D.S., Leal, M., 2016. Visual motion detection and habitat preference in *Anolis* lizards. *J. Compar. Physiol.* 202, 783–790.
- Torres, J.A., Snelling, R.R., 1997. Biogeography of Puerto Rican ants: a non-equilibrium case? *Biodivers. Conserv.* 6 (8), 1103–1121.
- Tribble, W., Carroll, R.O.N., 2014. Manipulating tropical fire ants to reduce the coffee berry borer. *Ecol. Entomol.* 39 (5), 603–609.
- Vazquez Moreno, L.L., Jiménez, E.B., Claro, O.E., Brito, Y.M., Simonetti, J.A., 2006. Observaciones sobre enemigos naturales de la broca del café (*Hypothenemus hampei* Ferrari) en Cuba. *Fitosanidad* 10 (4), 307–308.
- Vitt, L.J., Avila-Pires, T.C.S., Zani, P.A., Sartorius, S.S., Espósito, M.C., 2003. Life above ground: ecology of *Anolis fuscoauratus* in the Amazon rain forest, and comparisons with its nearest relatives. *Can. J. Zool.* 81 (1), 142–156.
- Wetterer, J.K., Porter, S.D., 2003. The little fire ant, *Wasmannia auropunctata*: distribution, impact and control. *Sociobiology* 41 (3), 1–41.