Ecological Entomology (2014), DOI: 10.1111/een.12139

Manipulating tropical fire ants to reduce the coffee berry borer

WARING TRIBLE¹ and RON CARROLL² ¹The Rockefeller University, New York, New York, U.S.A. and ²Odum School of Ecology, University of Georgia, Athens, Georgia, U.S.A.

Abstract. 1. The coffee berry borer *Hypothenemus hampei* (Coleoptera, Curculionidae) (Ferrari) is the most important pest of coffee production worldwide.

2. The hypothesis that the tropical fire ant, *Solenopsis geminata* Westwood, indirectly protects the coffee berry borer by suppressing other ant species that are the coffee berry borer's primary predators was tested.

3. It was found that removing *S. geminata* from coffee plots significantly increased the disappearance of adult coffee berry borer beetles from coffee berries compared with control plots. An average of 6% of beetles disappeared from plots with *S. geminata* whereas 23% of beetles disappeared from plots from which *S. geminata* was removed. This pattern was observed on two shade coffee farms with marked differences in ant species composition, one in the rainforest in central Costa Rica and one in the cloudforest in northwest Costa Rica.

4. If the results of this small-scale study can be replicated on the farm level, then *S. geminata* suppression may represent a new management technique for the coffee berry borer throughout Central and South America.

Key words. Biological control, coffee berry borer, fire ant, Formicidae, *Hypothenemus hampei*, *Solenopsis*.

Introduction

Coffee is the second most important commodity in the world by value, and the coffee berry borer is a beetle that constitutes the most important pest in coffee production worldwide (Damon, 2000). It is estimated that the coffee berry borer causes approximately \$500 million worth of damage yearly (Chapman *et al.*, 2009). Traditional control of the coffee berry borer requires extensive application of pesticides, which makes biological control, controlling pests with predators, parasites, and pathogens, a much sought-after alternative (Vega *et al.*, 2009).

Biological control of the coffee berry borer has been attempted using a number of organisms: parasitoid wasps, entomopathogens, and ants (Vega *et al.*, 2009). Ants can enter the coffee berry and attack embedded beetles, and may therefore serve an important role in reducing the dry-season population of coffee berry borer beetles (Larsen & Philpott, 2010). In the dry season, coffee berry borer beetles survive in coffee berries remaining on the bush and on the ground. Many farmers remove all coffee berries from the bushes at the end of the season to reduce this resource for berry borers, but it is difficult to locate

Correspondence: Waring Trible, 1230 York Avenue, New York, NY 10065, U.S.A. E-mail: wtrible@rockefeller.edu

an important role in reducing dry season coffee berry borer populations and minimising future outbreaks (Armbrecht & Gallego, 2007; Jaramillo *et al.*, 2007; Chapman *et al.*, 2009; Vélez *et al.*, 2006). No regimes have been devised to augment this ant-based predation, however, and one recent review suggested that manipulating ant populations to increase predation of the coffee berry borer would be extremely difficult (Vega *et al.*, 2009). Nevertheless, a few ant species are considered important

coffee berries in the soil, and soil-dwelling ants may thus play

Nevertheless, a few ant species are considered important predators of the coffee berry borer (Armbrecht *et al.*, 2005; Armbrecht & Gallego, 2007). The tropical fire ant, *Solenopsis geminata* Westwood, preys on free-living coffee berry borer beetles, but is not known to penetrate coffee berries and prey on embedded beetles (Varón *et al.*, 2004). *Solenopsis geminata* is a highly dominant ant species from Mexico to Brazil, however, and it is also possible that *S. geminata* indirectly protects the coffee berry borer by suppressing other ant species that may exert more efficient predation pressure. Indeed, some studies have shown that *S. geminata* prevalence is inversely correlated with ant diversity, and that *S. geminata* removal can lead to an increase in many arthropod species, including other ants (Risch & Carroll, 1982; Perfecto, 1991; Philpott *et al.*, 2006a, but see Perfecto, 1994). We hypothesised that a greater number of coffee berry borer beetles would disappear (be preyed upon) from coffee plots without *S. geminata* than from plots with *S. geminata*. This species is particularly relevant because *S. geminata* is one of a few ants that attains a high population density in both 'sun' and 'shade' coffee plantations because of its large geographical range (Perfecto and Snelling, 1995; Philpott *et al.*, 2006a; Varón *et al.*, 2007). If *S. geminata* removal represents a viable control strategy for the coffee berry borer, the procedure may be applicable throughout much of Central and South America across a wide variety of coffee management types.

We tested the hypothesis that *S. geminata* indirectly protects coffee berry borer beetles on two coffee farms in Costa Rica by monitoring ant populations using tuna fish baits in 12 plots and selectively removing *S. geminata* with an organophosphate pesticide in six randomly assigned experimental plots, then measuring the disappearance of coffee berry borer beetles from coffee berries in experimental and control plots over a 72-h period.

Materials and methods

Farm selection

During the rainy season (July to August) 2011, we performed *S. geminata* removal experiments on two shade coffee farms in Costa Rica. *Finca Leon y Parra*, 'Farm 1,' is located in Monteverde (cloudforest) at 1100 m above the mean sea level (msl) and *Aquiares*, 'Farm 2,' is located near Turrialba at 1000 m above msl. The experiment was conducted during the rainy season because previous studies have shown that beetle predation by ants is highest during this period (Gallego Ropero & Armbrecht, 2005; Armbrecht & Gallego, 2007). Both coffee farms had moderate shade cover (as in Philpott *et al.*, 2006b) with a small number of shade tree species at low density and active pesticide regimes. However, the two farms differed based on temperature and the ant species assemblages observed and were thus chosen to test the hypothesis in two ecologically distinct agroecosystems.

Plot design

On each farm, six 5×5 m plots were designated and randomly assigned to 'with *S. geminata*' (control) and 'without *S. geminata*' (experimental) treatments. One control plot in Farm 1 was discarded owing to an unusually low initial activity of *S. geminata* (see *Discussion*), resulting in a total of 11 plots used for analysis in this study.

The plots selected on both farms contained 12-15 coffee bushes, in three rows spaced approximately 2 m apart with five bushes per row, spaced approximately 1 m apart. Plots were chosen so as to standardise *S. geminata* occurrence and activity.

Pesticide application and berry placement

Each 5×5 m plot contained a 2×2 m 'inner plot area' surrounded by a 1.5-m-wide border ('outer plot area') as shown in

Fig. 1. Plots were arranged such that each contained one or two *S. geminata* mounds with a diameter between 20 and 50 cm in the 1.5-m-wide outer plot area only (see Fig. 1).

Control plots were baited in the morning, then coffee berries containing coffee berry borer beetles were placed in the 2×2 m inner area of the plots in the afternoon. All experimental plots were baited in the morning, and then an organophosphate pesticide (Lorsbon-15G, active component 15% Chlopyrifos) was applied directly to the *S. geminata* mounds in the outer plot areas in the afternoon. This was repeated on the following day, then on the third day experimental plots were baited in the morning and coffee berries were placed in 2×2 m inner plot areas in the afternoon. These three sequential baitings were used in experimental plots to verify *S. geminata* removal.

Plots were designed to prevent spillover effects: in experimental plots, pesticide was applied only to *S. geminata* mounds located only in the outer plot area, whereas coffee berries containing coffee berry borer beetles were placed only in the inner plot area. Coffee berries were not placed in plots until 24 h after final pesticide treatment and were placed in small aluminum dishes to prevent direct contact with the ground. Two treatments of pesticide were used to allow small amounts of pesticide to be applied to the fire ant mounds at each application, which may have resulted in less potential for pesticide to leach into the inner plot area.

Baiting regime and activity index

Plots were systematically baited using tuna fish baits, according to the methods of Perfecto (1994). Tuna fish baits were placed every 1 m in the outer plot area and every 50 cm in the inner plot area, resulting in 57 baits per plot, as in Fig. 1. Each bait consisted of ~1.3 g of tuna placed in the centre of a small Petri dish and left in the field for 20 min. Petri dishes were used for the baits so that tuna could be removed after baiting to prevent any lasting effect of tuna placement on the plot. After 20 min, the baits were collected and ant activity was recorded, using an 'activity index' as in Perfecto, 1994.

Species presence on the bait was recorded and rated as I, II, or III, where I represents 1–10 ants, II represents 11–20, and III represents >20, according to the methods of Perfecto, 1994. Where multiple species were observed on a single bait, the presence of each species was rated individually. These activity index values were summed for each plot and compared using the Mann–Whitney *U*-test. All baiting occurred before 13.00 hours. Ants observed on the baits were grouped into morphospecies using a $10 \times$ hand lens in the field. Species represented on only a single bait were not included in this analysis. Multiple vouchers of all other species were collected, and species or genus identities were confirmed with the aid of taxonomists at Costa Rica's *Instituto Nacional de Biodiversidad* and *Universidad de Costa Rica*.

Coffee berry placement and determination of change in beetle abundance

For each plot, 60 immature (green) coffee berries with visible coffee berry borer damage were collected [berries used were as



Fig. 1. Design of 5×5 m plots. All *Solenopsis geminata* mounds (one or two per plot) were located in the 1.5-m-wide outer plot area; pesticide was applied only in this area. Tuna fish baits were placed every 1 m in the 1.5-m-wide outer plot area and every 50 cm in the 2×2 m inner plot area, for a total of 57 baits. To prevent pesticide applied to *S. geminata* mounds from reaching coffee berry borers, coffee berries were placed in aluminum dishes only in the inner plot area 24 h after pesticide was applied. Ten of the 25 bait locations in the inner plot area were randomly selected for coffee berry placement, with three berries at each location.

in Larsen & Philpott (2010)]. These immature berries typically contain one adult female coffee berry borer beetle. Thirty berries were randomly selected and opened to determine the 'initial' number of adult coffee beetles per berry. Initial value was calculated as:

Initial beetles per berry = number of beetles observed /number of berries opened

The remaining 30 berries for each plot were placed in the field for 72 h. Ten of the 25 positions in the inner portion of the plot that were originally used for tuna fish baiting were randomly selected, and three coffee berries with berry borer damage were placed in a small aluminum dish in each selected location (Fig. 1). This method was chosen because it allowed us to compare the ants that were found in a given location

with the berry borer removal that was later observed at that location, and thus test the potential for small-scale effects of ant species presence on berry borer removal. It should also be noted, however, that placing coffee berries in locations that contained tuna fish baits 24 h previously may have produced greater berry borer removal owing to greater activity of mass-foraging ants. Tuna baits were placed in a Petri dish and removed after sampling to reduce this possibility.

After 72 h, the 30 berries were collected from each plot, all berries were opened, and the 'final' number of beetles per berry was calculated as:

Final beetles per berry = *number of beetles observed*

[number of berries opened]

For both *initial beetles per berry* and *final beetles per berry*, all beetles, alive and dead, and all substantial fragments of beetles

(>50%) were recorded as one beetle present. A metric called Δb was then calculated for each plot as:

$\Delta b = (initial number of beetles per berry$ -final number of beetles per berry) /initial number of beetles per berry.

 Δb represents the proportion of beetles that disappeared from coffee berries after 72 h in the field; a Δb value of 1 indicates that all beetles disappeared after 72 h whereas a Δb value of 0 indicates that no change occurred between the initial and final number of beetles per berry. $\Delta b \times 100\%$ gives the percentage of beetles that disappeared from coffee berries after 72 h. It was possible to observe negative values of Δb through sampling error. Initial berries, opened immediately, and final berries, opened after 72 h in the field, were selected randomly from the same pool, but if by chance the initial berries opened had a low number of beetles per berry and very few beetles disappeared after 72 h in the final berries, Δb could be negative.

We hypothesised that Δb values would be greatest in experimental plots, meaning that more beetles would disappear from experimental than control plots, presumably owing to predation. The Δb metric was used to control for any variability in the number of beetles in the collected berries; the proportion of disappearance was considered rather than the total number of beetles that disappeared to compensate for the fact that batches of berries collected from the field, particularly those from different farms, may have contained different average numbers of beetles. Δb values were compared statistically between experimental and control plots using Wilcoxon's rank sum test.

Results

S. geminata exclusion

Ant activity was monitored using tuna fish baits on Day 1 in control plots, and, to verify *S. geminata* removal, on Day 1, Day 2, and Day 3 in experimental plots. In the inner plot area, experimental plots showed significantly reduced *S. geminata* activity, both between Day 1 and Day 3 baitings in the experimental plots (P < 0.005; see Fig. 2), and in Day 3 baitings in experimental plots compared with Day 1 baitings in control plots (P < 0.01). Pesticide application did not significantly decrease the pooled activity of other ant species. In fact, a slight increase was observed in the activity of ants other than *S. geminata* after pesticide application, although this increase was not significant (Fig. 2).

Δb values

 Δb values were significantly greater in experimental plots than in control plots (P > 0.05; Fig. 3). An average of 6% of adult beetles disappeared after 72 h from control plots ($\Delta b = 0.056 \pm 0.124$; mean ± 1 SD), whereas 23% of beetles disappeared from experimental plots ($\Delta b = 0.234 \pm 0.029$). Table 1. Ant species observed on Farm 1 and Farm 2 during this study.

Species on Farm 1 (cloudforest, Monteverde)	Species on Farm 2 (rainforest, Turrialba)	Species on both farms (Not necessarily on all plots)
Brachymyrmex sp.	Brachymyrmex sp. 2	Wasmannia auropunctata
Linepithema neotropicum	Odontomachus sp.	Solenopsis sp.
Pheidole sp.	Nylanderia steinheili	
Pheidole sp. 2	Pheidole radoszkowskii	
Pheidole sp. 3	Pheidole sp. 5	
Pheidole sp. 4	<i>Pheidole sp. 6</i> <i>Solenopsis picea</i> Formicidae <i>sp.</i>	

Species diversity

A total of 16 ant species, excluding *S. geminata*, were collected from the tuna fish baits between the two farms (Table 1). Only two species were observed on both farms, whereas six species were observed only on Farm 1 (cloudforest) and eight species were observed only on Farm 2 (rainforest).

Ten of the 16 species were identified to genus and five to species (Table 1). Vouchers of one species, Formicidae *sp.*, were damaged and could not be identified to genus. All genera identified, except for *Odontomachus*, contain species considered potential predators of the coffee berry borer (Bustillo *et al.*, 2002). Of the five identified species, four of them, *Nylanderia steinheili* Forel, *Pheidole radoszkowskii* Mayr, *Solenopsis picea* Emery, and *Wasmannia auropunctata* Roger, are considered predators of the coffee berry borer (Vázquez *et al.*, 2006; Armbrecht & Gallego, 2007). Interestingly, *W. auropunctata* was the only known coffee berry borer predators were found exclusively on Farm 2.

Species presence, activity, and diversity associations with Δb values

The activity of ant species at each of the tuna fish baits within the plots was recorded, which allowed us to test whether the presence or absence of any species in a plot was significantly associated with Δb values. We also recorded which species were present at the tuna fish bait locations where berry borers were placed 24 h later and tested whether the presence or absence of any species at these specific locations had a significant association with Δb values at that location. We did not find a significant association for either of these measures for any species (i.e. no ant species presence or abundance was significantly associated with coffee berry borer removal). No association was also seen between total abundance or diversity of ant species and Δb values on experimental plots.



Fig. 2. Pooled inner plot area activity indices across all experimental plots for *Solenopsis geminata* and for all other ant species. Pesticide was applied to *S. geminatae* mounds in the outer plot area after sampling on Day 1 and Day 2.

Discussion

These results may inspire a novel partial control strategy for the coffee berry borer. Although we did not specifically implicate ant predation for the higher Δb values observed in experimental plots, this assumption has been reasonably made in other studies (Varón *et al.*, 2004, but see Vega *et al.*, 2009). A greater number of coffee berry borer beetles disappeared after 72 h in experimental than in control plots, likely through the mechanism of greater predation pressure by other ants after the removal of *S. geminata*. This is, as far as we know, the first time ants have been experimentally manipulated to increase natural enemy effects on the coffee berry borer.

Of the 16 ant species observed other than *S. geminata*, only 2 were observed on both farms (Table 1). This ~75% difference in ant species composition between the two farms is especially interesting considering the consistency of Δb values: it is possible that *S. geminata* removal may represent a generalised approach to coffee berry borer control rather than being specific to particular ant assemblages. The fact that Δb values were consistent between the two farms in spite of the differing ant assemblages may also indicate that none of the species observed are vital for coffee berry borer removal; other, unknown predators may also play a role.

This is not the first time that an indirect interaction has been studied in reference to coffee berry borer control. An ant-hempiteran mutualism involving *Azteca instabilis* (Smith) can benefit coffee production by increasing ant foraging on the coffee bush and thereby increasing removal rates of coffee berry borer beetles (Vandermeer *et al.*, 2002; Perfecto & Vandermeer, 2006). Other studies have shown that twig-nesting ant species, which forage directly on the bush, may also be important predators of the coffee berry borer (Armbrect & Perfecto, 2003; Larsen & Philpott, 2010). These findings, in conjunction with ours, suggest a number of measures that could potentially maximise ant-based predation of the coffee berry borer: encouraging *A. instabilis* and its coccid symbiont, increasing the number of habitats for twig-nesting ants, and reducing *S. geminata* populations.

The 'fire ant wars' of S. invicta in the United States make us hesitant to suggest that fire ants can or should be permanently removed from any system (Tschinkel, 2006). It is possible, however, that S. geminata could be systematically suppressed at strategic times to benefit coffee production. For example, in Colombia the system of 're-re' is often employed to collect all possible coffee berries at the end of the growing season and thereby reduce potential habitats for coffee berry borer beetles over the dry season (Armbrecht & Gallego, 2007; Chapman et al., 2009). If this action were combined simultaneously with steps to suppress S. geminata, it may be possible to reduce surviving beetles in the berries that are not located and remain on the ground. Solenopsis geminata suppression in this study was achieved through the use of organophosphate pesticide, but boiling water has also been successfully used to control fire ants, and may provide an alternative acceptable for organic farmers (Tschinkel & King, 2007). Another alternative to organophosphate pesticide may be Avermictin, a biological toxin that largely works as a stomach poison specific to the genus Solenopsis. These conclusions are speculative, however, and further investigation will be required before this method can be applied at the farm scale. Coffee berry borer removal was observed to increase in this small-scale study, but ant predation was not explicitly demonstrated. Furthermore, no economic considerations were made, and it is not known whether the cost of pesticide for S. geminata removal might outweigh any benefit in increased coffee berry borer predation. Finally, we



Fig. 3. Δb for each experimental and control plot in Farm 1 (left side) and Farm 2 (right side). Experimental plots had significantly higher Δb values, indicating that a greater number of beetles disappeared from coffee berries. Note that negative values of Δb were possible via sampling error and that the outlier plot from Farm 1 is excluded.

only recorded disappearance of adult beetles in berries on the ground, but berries still on the bush and eggs and larvae should also be considered.

It is interesting that *S. geminta* appears to act antagonistically with respect to pest biological control within the coffee agroecosystem, considering that *S. geminata* and other fire ants generally have been considered, and sometimes deployed, as biological control agents in other systems (Risch *et al.*, 1982; Nestel & Dickschen, 1990; Philpott, 2006; Way & Heong, 2009). This interaction of *S. geminata* and the coffee berry borer might be a special case, however, for the simple reason that *S. geminata* workers may be too large to penetrate the coffee berry and efficiently remove coffee berry borer beetles (Varón *et al.*, 2004; Armbrecht & Gallego, 2007).

This study focused on ant predation, but other mechanisms may have also caused the increased disappearance of berry borer beetles. We cannot rule out the fact that experimental plots had pesticide application whereas control plots did not. Pesticide application may have caused the observed increase in berry borer disappearance by causing the beetles to exit the berries. We took measures to explicitly control for this possible effect, however, and do not expect that it had a significant influence on the results. One indication that pesticide application may have not affected coffee berry borer beetles is that pooled activity of ant species other than *S. geminata* did not significantly decrease after pesticide application in control plots, both in the outer plot areas where pesticide was applied and in the inner plot area

An additional fact may support his opinion. One of the control plots in Farm 1 had extremely low *S. geminata* activity and was not used for data analysis. Nonetheless, this control plot provided something of a 'natural experiment' because it contained extremely low *S. geminata* activity, which made it more akin to an experimental plot. Fitting with our hypothesis, this plot had the highest Δb value observed: 0.560. Thus, the plot with the naturally lowest *S. geminata* activity also had the highest disappearance of coffee berry borer beetles, independent of pesticide application.

Experimental plots also had three tuna fish baitings whereas control plots only had one, which may have biased out results toward mass-foraging ants. This, however, is likely to bias our results against the hypothesis, as it would inflate activity of any remaining *S. geminata* in experimental plots. It is also possible that non-ant predators were responsible for the greater disappearance of borers in experimental than control plots, or that this enhanced disappearance was mediated by some non-predatory factor.

Solenopsis geminata is a highly dominant ant species throughout Mexico, Central America, and much of northern South America. In this study, we demonstrated increased disappearance of the coffee berry borer after *S. geminata* removal on two ecologically dissimilar coffee farms, which shared fewer than 25% of observed ant species. The fact that similar results were observed on both farms may indicate that *S. geminata* performs an overall protective role of the coffee berry borer that is not specific to either of the ant assemblages studied. If this is the

case, then *S. geminata* removal may represent a novel partial control technique in coffee farms throughout Central and South America. The fact that *S. geminata* attains a high population density across the range of coffee management intensity provides an optimistic outlook for *S. geminata* removal across sun coffee farms as well, but this claim will need to be tested. Although still highly tentative, this and other studies provide a novel look at the suite of ant-based control measures which may be taken against the coffee berry borer.

Acknowledgements

I am eternally indebted to Ken Ross for his mentorship and support throughout my undergraduate. I wish to thank Rebecca de Jesus for helping me meet farmers in Costa Rica, to thank Scott Connely and Lindsay Stallcup for logistical assistance, and to give an enormous thanks to Paul Hanson and Manuel Solis for instruction on taxonomy and verifying my identifications. I would further like to thank Inge Armbrecht for useful comments on an early draft of this manuscript. Finally I would like to thank Ron Carroll, for stewarding me through this project, and my funding sources, The University of Georgia Foundation Fellowship and the P.W. Fattig Entomology Scholarship.

References

- Armbrecht, I. & Gallego, M.C. (2007) Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata*, **124**, 261–267.
- Armbrecht, I. & Perfecto, I. (2003) Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. *Agriculture, Ecosystems & Environment*, **97**, 107–115.
- Armbrecht, I., Rivera, L. & Perfecto, I. (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of colombian coffee plantations. *Conservation Biology*, **19**, 897–907.
- Bustillo, A.E., Cárdenas, R. & Posada, F.J. (2002) Natural enemies and competitors of *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in Colombia. *Neotropical Entomology*, **31**, 635–639.
- Chapman, E.G., Jaramillo, J., Vega, F.E. & Harwood, J. (2009) Biological control of coffee berry borer: the role of DNA-based gut-content analysis in assessment of predation. Proceedings of the 3rd International Symposium on Biological Control of Arthropods, *February* 8-13, 2009, Christchurch, New Zealand (ed. by P.G. Mason, D.R. Gillespie and C. Vincent), pp. 475-484. USDA-FHTET, Morgantown, West Virginia.
- Damon, A. (2000) A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin* of Entomological Research, **90**, 453–466.
- Gallego Ropero, M. & Armbrecht, I. (2005) Depredación por hormigas sobre la broca del café *Hypothenemus hampei* (Curculionidae: Scolytinae) en cafetales cultivados bajo dos niveles de sombra en Colombia. *Manejo Integrado de Plagas y Agroecologia*, **76**, 32–40.
- Jaramillo, J., Borgemeister, C. & Baker, P. (2007) Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies. *Bulletin of Entomological Research*, 96, 223–233.
- Larsen, A. & Philpott, S.M. (2010) Twig-nesting ants: the hidden predators of the coffee berry borer in Chiapas, Mexico. *Biotropica*, 42, 342–347.

- Nestel, D. & Dickschen, F. (1990) The foraging kinetics of ground ant communities in different mexican coffee agroecosystems. *Oecologia*, 84, 58–63.
- Perfecto, I. (1991) Dynamics of solenopsis geminata in a tropical fallow field after ploughing. *Oikos*, 62, 139–144.
- Perfecto, I. (1994) Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. *Oecologia*, **98**, 184–192.
- Perfecto, I. & Snelling, R. (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications*, 5, 1084–1097.
- Perfecto, I. & Vandermeer, J. (2006) The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. Agriculture, Ecosystems & Environment, 117, 218–221.
- Philpott, S. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, **31**, 369–377.
- Philpott, S.M., Perfecto, I. & Vandermeer, J. (2006a) Effects of management intensity and season on arboreal ant diversity and abundance in coffee agroecosystems. *Biodiversity and Conservation*, 15, 139–155.
- Philpott, S.M., Uno, S. & Maldonado, J. (2006b) The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodiversity and Conservation*, 15, 487–501.
- Risch, S.J. & Carroll, C.R. (1982) Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology*, 63, 1979–1983.
- Risch, S.J., Carrol, C.R. & Url, S. (1982) The ecological role of ants in two mexican agroecosystems. *Ecology*, 55, 114–119.
- Tschinkel, W.R. (2006) *The Fire Ants*. Harvard University Press, Cambridge, Massachusetts.
- Tschinkel, W.R. & King, J.R. (2007) Targeted removal of ant colonies in ecological experiments, using hot water. *Journal of Insect Science*, 7, 1–12.
- Vandermeer, J., Perfecto, I., Nuñez, G.I. & Phillpott, S. (2002) Ants (Azteca sp.) as potential biological control agents in shade coffee production in Chiapas, Mexico. Agroforestry Systems, 56, 271–276.
- Varón, E.H., Hanson, P., Borbón, O., Carballo, M. & Hilje, L. (2004) Potencial de hormigas como depredadoras de la broca del café (*Hypothenemus hampei*) en Costa Rica. *Manejo Integrado de Plagas* y Agroecologia, **73**, 42–50.
- Varón, E.H., Hanson, P., Longino, J.T., Borbón, O., Carballo, M. & Hilje, L. (2007) Distribución espacio-temporal de hormigas en un gradiente de luz, dentro de un sistema agroforestal de café, en Turrialba, Costa Rica. *Revista de Biología Tropical*, **55**, 943–956.
- Vázquez, L.L., Blanco, E., Elósegui, O., Matienzo, Y. & Alfonso, J. (2006) Observaciones sobre enemigos naturales de la broca del café (Hypothenemus hampei Ferrari) en Cuba. *Fitosanidad*, **10**, 307–308.
- Vega, F.E., Infante, F., Castillo, A. & Jaramillo, J. (2009) The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): a short review, with recent findings and future research directions. *Terrestrial Arthropod Reviews*, 2, 129–147.
- Vélez, M., Bustillo, A. & Posada, F. (2006) Depredación de Hypothenemus hampei por hormigas, durante el secado solar del café. Cenicafé, 57, 198–207.
- Way, M.J. & Heong, K.L. (2009) Significance of the tropical fire ant *Solenopsis geminata* (Hymenoptera: Formicidae) as part of the natural enemy complex responsible for successful biological control of many tropical irrigated rice pests. *Bulletin of Entomological Research*, 99, 503–512.

Accepted 20 May 2014