COMMUNITY AND ECOSYSTEM ECOLOGY

Indirect Interactions Between Ant-Tended Hemipterans, a Dominant Ant *Azteca instabilis* (Hymenoptera: Formicidae), and Shade Trees in a Tropical Agroecosystem

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Environ. Entomol. 37(3): 734–740 (2008)

ABSTRACT The occurrence, intensity, and composition of mutualisms are dependent not only on the co-occurrence of mutualists, but also the broader biotic context in which they are embedded. Here, the influence of the specific nest tree identity of the ant *Azteca instabilis* (F. Smith) on the density of the green coffee scale (*Coccus viridis* Green) was studied in a coffee agroecosystem in southern Mexico. The hypothesis that an indirect competitive interaction for ant attendance occurs between a scale species (*Octolecanium* sp. Kondo) in the canopy of the shade tree *Inga micheliana* Harms and *C. viridis*, which inhabits coffee bushes (*Coffea arabica*) beneath the shade trees was tested. Coffee bushes beneath a different shade tree species (*Alchornea latifolia* Swartz) were used as an indication of *C. viridis* density in a noncompetitive environment. Results indicate that *C. viridis* occurs in significantly lower density adjacent to nests in *Inga*, supporting the hypothesis of indirect competition. Additional experimentation suggests that there is a mutualism between *Azteca* and *Octolecanium* and that this interaction may be mediated by a hierarchy in ant attendance of scale insects. Our results show the importance of considering the biotic context of ant–hemipteran mutualisms. In coffee agroecosystems, consideration of shade tree diversity and species composition may be directly applicable to the biological control of insect pests.

KEY WORDS mutualism, indirect competition, shade coffee, scale insects, biological control

Ant–hemipteran associations have been well documented in the neotropics (Buckley 1987, Dansa and Rocha 1992, Oliveira and Del-Claro 2005). Many such associations involve ant genera that apparently obtain nearly all their nitrogen from sugar secretions (Davidson et al. 2003). These ants visit extrafloral nectaries (EFNs) and tend honeydew-producing insects including hemipterans and/or lepidopterans (Hunt 2003, Blüthgen et al. 2004). Ant-tending provides protection from predation, desiccation, and/or fungal growth for the tended insects, thus creating a mutualistic interaction between the two (Way 1963, Hölldobler and Wilson 1990). The factors that determine which ant species use which carbohydrate resources can largely be attributed to the hierarchy of interspecific behavioral dominance. Dominant ant species tend to monopolize high-quality and permanent honeydew sources (such as hemipteran aggregations), whereas subdominant species either visit EFNs/lepidopterans or precede dominant ants at hemipterans before displacement occurs (Blüthgen et al. 2004). However, the factors that determine what hemipteran species (or assemblage) is tended by a dominant ant are less well understood.

Numerous factors have been suggested as determinants of both species composition and tending intensity of ant-tended hemipteran aggregations. These include host plant density (Addicott 1979, Itioka and Inoue 1996), the presence of EFNs (Offenberg 2000), host plant quality (Auclair 1963, Breton and Addicott 1992), differences in colony distance to the nest (Fischer et al. 2001), species-specific differences between hemipterans and ants (Addicott 1978, Bristow 1984, Fischer et al. 2001), relative densities of hemipterans (Sakata 1999), and seasonality in the level of honeydew demand by ants (Sudd and Sudd 1983, Bristow and Yanity 1999, Fischer et al. 2001). These factors are further mediated by differences in the quality of hemipteran honeydew resources and host plant type (Fischer et al. 2001). Generally, the biotic context of mutualisms strongly determines their strength and patterns of occurrence (Cushman and Addicott 1989).

Ants should be expected to respond most intensively to the most profitable honeydew resources during collection activity (Davidson 1978, Nonacs and Dill 1990, Mailleux et al. 2000). Such collection behavior may lead to indirect ant-mediated competition between hemipterans for the mutualistic services that ants provide (Fischer et al. 2001). However, given that

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0046-225X/08/0734–0740$04.00/0

certain ant species opportunistically use a range of hemipteran species within diverse plant communities, the occurrence of indirect competition is also likely to be strongly dependent on biotic context.

In a shaded coffee agroecosystem in Southern, Mexico, the role of ant-tended hemipteran species, plant diversity, and ant-tending behavior in generating context-dependent indirect competition was studied. Here, the numerically dominant arboreal ant species is *Azteca instabilis* (F. Smith) (Philpott et al. 2004). *Azteca* is found nesting on ≈2.6%, or ≈276 of ≈10,597, of the shade trees in the canopy (Vandermeer and Perfecto 2006). The most commonly inhabited shade tree species within our system are *Alchornea latifolia* Harms (Euphorbiaceae) (11% of all nests) and *Inga micheliana* Swartz (Fabaceae) (45% of all nests). These species are also the most abundant in this agroecosystem, because *A. instabilis* selects nest trees without preference (Vandermeer et al. 2008).

In the study system, a common scale insect is the green coffee scale, *Coccus viridis* Green, which is found at high density in coffee bushes, *Coffea arabica* (Rubiaceae), growing adjacent to the shade trees in which *Azteca* nests (Vandermeer and Perfecto 2006). Although it has been documented that *C. viridis* is found in high abundance in the proximity of *Azteca* (Vandermeer and Perfecto 2006), additional secondary factors influencing the population density of this scale insect have not previously been studied. *Azteca* is known to tend a diversity of hemipteran species (Davidson et al. 2003), the ubiquitous species in this case being *C. viridis* and *Octolecanium* sp. Kondo. *Octolecanium* is found in the proximity of *Azteca* nests at comparable distance to that of *C. viridis;* however, they inhabit the canopy of the *Inga* nest tree and never the coffee bushes. Thus, there is a distinct spatial segregation between these coccids that precludes the possibility of direct competitive interactions for phloem resources.

Critically, *Azteca* nests in *Inga* are found in association with infestations of *Octolecanium,* whereas *Alchornea* only rarely contains scales in the canopy (see Results). Therefore, when nesting in *Alchornea, Azteca* should be expected to tend *C. viridis* on nearby coffee bushes with greater intensity than on coffee bushes near to individuals of *Inga* where the alternative *Octolecanium* is available. If true, this would indicate that *Octolecanium* exerts competitive pressure on *C. viridis,* but through the indirect mechanism of the ant mutualism. Data on scale insect density, ant activity, and tending behavior at two different shade tree species (*Alchornea* and *Inga*) were collected to test the hypothesis that the mutualism between the scale insect, *C. viridis,* and the ant, *Azteca,* is eliminated as a result of ant-mediated indirect competition with another scale insect, *Octolecanium.*

Materials and Methods

The study was conducted on a traditional organic shaded coffee agroecosystem in the Soconusco region of Chiapas, Mexico (15°10′ N and 92°20′ W). A 45-ha plot was used to survey ant nests. This plot is the site of ongoing research on the spatial ecology of *Azteca* and is representative of the farm as a whole (≈300 ha in size). The system is diverse, with ≈200 species of shade trees, but predominantly several species in the genus *Inga* and *Alchornea latifolia* (Vandermeer et al. 2002).

Coccus viridis populations near *Azteca* nests were sampled to infer the strength of the *Azteca–Coccus* mutualism. Twenty-six trees with *Azteca* nests were selected: 10 *Inga micheliana,* 11 *Alchornea latifolia,* and 5 *Yucca guatemalensis* Baker (Liliaceae). *Yucca guatemalensis,* although not a common species on the farm, was selected for its low stature and accessible canopy. This third species was included as a point of comparison to *Alchornea* because it appeared to lack canopy scales in preliminary observations. An additional three *Alchornea* and three *Inga* trees were also randomly selected for canopy surveying. Trees were randomly selected from a sampling pool that had been recorded with *Azteca* nests for four surveys over a 2-yr period within the 45-ha plot. This control diminished the likelihood that *C. viridis* density would be abnormally low because of recent nest colonization or imminent death. Nest trees of the same species within clusters of nests (Vandermeer et al. 2008) were discarded from the sampling pool to avoid pseudoreplication.

At each tree, scale density at every coffee bush within a 2-m radius of the bole at its widest point was determined. Scale density was estimated using the protocol described in Perfecto and Vandermeer (2006). Circumference of each tree was measured as the diameter at breast height (dbh). In addition, the presence or absence of arboreal scales was determined using a canopy level binocular scan (the trees were invariably on steep slopes) and by cutting leaf and branch samples at various heights from the canopy of each tree. Under our hypothesis, tending activity should be higher in coffee beneath *Alchornea* than *Inga.* Ant activity and the proportion of bushes with *Azteca* was also surveyed beneath nine *Inga* and nine *Alchornea* to a radius of 2 m. Activity was measured as the number of ants that crossed a central stem in a 1-min period at each coffee plant.

Previous work has shown that *C. viridis* is involved in a mutualistic interaction with *Azteca* (Vandermeer and Perfecto 2006). Therefore, experimentation was required only with *Octolecanium* to determine whether a mutualism was occurring. Ant exclusion experiments were conducted to verify the *Azteca–Octolecanium* mutualism and to test the prediction that the ants, if prevented from accessing *Octolecanium* scales in the *Inga* trees, would increase their tending activity of *C. viridis* in adjacent coffee bushes. Five *Inga* trees were selected to conduct these experiments, of which only one (a canopy height adult) was used to monitor ant activity levels. The four remaining trees were used to monitor changes in *Octolecanium* density. These trees were selected because their small stature (<4 m in height) and accessible canopies permitted observation of *Octolecanium* aggregations that

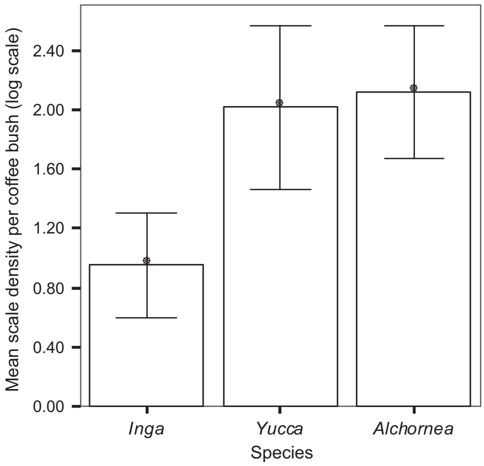

Fig. 1. Mean *C. viridis* density per coffee bush by tree species. Error bars represent 95% CIs.

was impossible in canopy height trees. All trees occurred within 15 m of each other.

Of the four small trees, two were selected as part exclusion and part control and the other two as complete exclusion depending on their suitability to Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) application. On one limb of each control tree, Tanglefoot was applied over a layer of plastic flagging (to avoid damage to the tree). This prevented ants from accessing the scale aggregations in that region of the tree. On experimental trees, Tanglefoot was applied across the trunk of the tree, excluding all access to scale aggregations. After the placement of Tanglefoot, a series of photographs were taken of the scale aggregations; at the time of application, 5 d after application, and 16 d after application. Four photographs were taken at experimental trees, and eight photographs were taken at controls (four on the exclusion portion, and four on the control). Change in scale density was determined by counting exact scale numbers in a set area of branch from digital photos. In addition, the prevalence of sooty mold was recorded by counting the number scales completely covered by sooty mold in each photograph. No significant differences in either scale numbers or sooty mold cover were observed between control and exclusion populations before experimentation.

Ant activity adjacent to the canopy height *Inga* was monitored both before and after the application of Tanglefoot to the trunk by counting the number of ants that crossed the visible portion of a point on every major stem (up to five stems) on all coffee bushes within 2 m of the nest tree. Count duration was dependent on activity levels but did not exceed 20 min for any one bush. Several counts were cancelled because of logistical constraints and extremely low activity levels resulting from dense fog.

Data were analyzed and graphs were generated using SPSS (v14 for Windows; SPSS, Chicago, IL). All count data were normally distributed or normal after log transformation. QQ plots were used to infer normality, and box plots were generated to test assumptions of equal population variance. Standard one-way analyses of variance (ANOVAs) or independent samples tests (depending on the number of factors) were used to compare differences between sample groups for the *C. viridis* density and ant activity survey and the exclusion experiments. A χ^2 table (generated in Microsoft Excel, v2002 for Windows; Microsoft, Redmond, WA) was used to compare the observed to the expected distribution of *Inga* and *Alchornea* trees with scales present in the canopy.

Table 1. **χ^2 table of canopy scale occurrence by tree species**

		Scales	No scales	Total
Observed	*Inga*	11	2	13
	Alchornea	3	10	13
	Total	14	12	26
Expected	*Inga*	7	6	13
	Alchornea	7	6	13
	Total	14	12	26
		P	0.0016	
		df = 1		

Results

Significant differences were found in *C. viridis* density in coffee bushes surrounding *Alchornea* versus *Inga* (independent samples test, $P < 0.001$; Fig. 1). The average log-transformed number of *C. viridis* per bush (non log-transformed means in parentheses) adjacent to *Alchornea* was 2.12 (344.65), whereas adjacent to *Inga* it was 0.95 (14.97). In coffee bushes adjacent to *Yucca,* there was an intermediate density of 2.02 (146.36). The density observed for *Inga* and *Yucca* represents a 96 and 58% reduction compared with *Alchornea,* respectively. However, the result for *Yucca* is only significantly different from *Inga* (independent samples test, $P < 0.01$) but not *Alchornea.* These levels compare with a background density (in areas without *Azteca* nests) of 14.29 (based on data reported in Vandermeer and Perfecto 2006). No significant correlation between tree circumference and *C. viridis* density in any of the three species was found. *Alchornea* is a species of larger average circumference than *Inga* and *Yucca* and thus greater potential *Azteca* nest size. However, the absence of a correlation indicates that our interspecific results are not confounded by this variable.

Surveying of nest tree canopies showed that 11 of 13 *Inga* trees surveyed had detectable densities of *Octolecanium* scales (and in some instances Pseudococcidae and Aleyrodidae pupa) in the canopy (Table 1). This result contrasts with only 3 of 13 *Alchornea* and 1 of 5 *Yucca* with detectable densities of scales in the canopy. Scales present in the *Alchornea* and *Yucca* canopies include two distinct, but as yet unidentified species (Coccidae), not found in *Inga* or coffee. No relationship between the presence or absence of other scale species in the canopy and density of *C. viridis* in coffee plants was detected either for *Alchornea* or *Yucca* (i.e., nests in *Alchornea* with canopy scales did

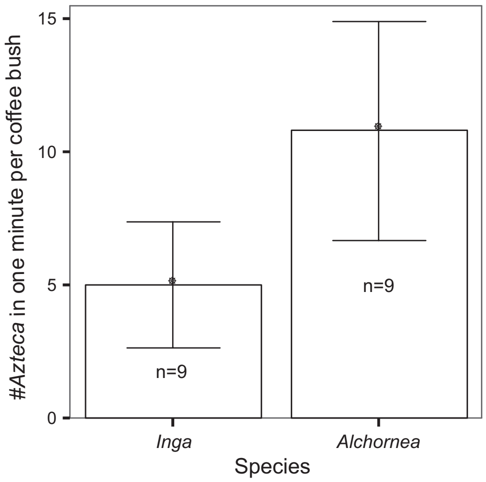

Fig. 2. Mean *Azteca* activity per coffee bush by tree species. Error bars represent 95% CIs.

not have lower *C. viridis* density than those located in trees without canopy scales). A χ^2 test showed that the observed distribution of trees with and without canopy scales within *Alchornea* and *Inga* is not likely to have occurred by chance (Table 1; $P < 0.01$).

Azteca activity (ants/min/bush) in the coffee layer was roughly double (10.0) beneath *Alchornea* as compared with *Inga* (5.0) (Fig. 2; independent samples test, $P < 0.01$). The proportion of coffee bushes showed a similar trend, with a mean of 74% of bushes with *Azteca* present beneath *Inga*, whereas this number approached 100% beneath *Alchornea* (Fig. 3; independent samples test, $P < 0.05$). Ant activity in coffee bushes beneath the adult *Inga* showed a significant positive correlation with number of days since canopy exclusion of ants (Fig. 4; $P < 0.05$, independent samples test). High variation in ant activity levels after 22 July may be a result of ant use of one coffee bush as a "bridge" to *Octolecanium* in an adjacent *Inga* tree. This use, however, occurred only for counts on 22 and 25 July before the branches were cut back. Our results here, it should be noted, are nonsignificant if these dates are removed from the analysis.

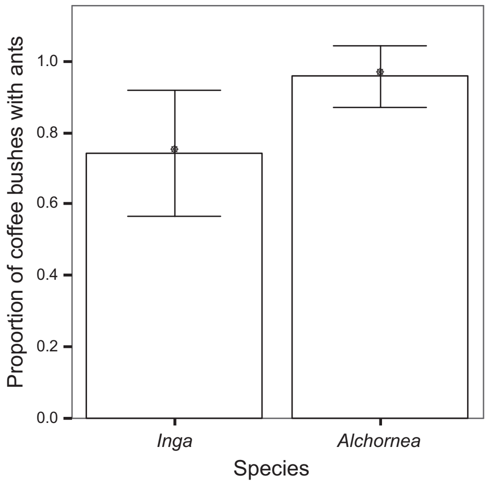

Fig. 3. Mean proportion of coffee bushes with *Azteca* present by tree species. Error bars represent 95% CIs.

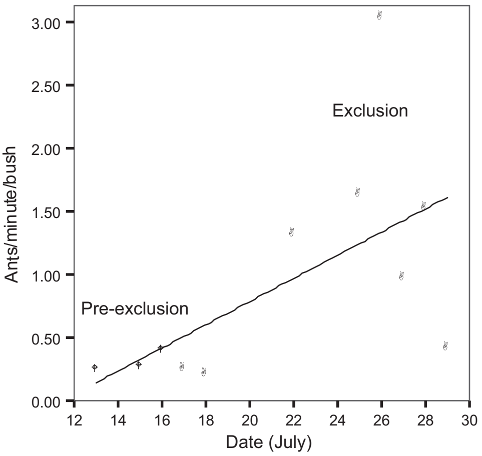

Fig. 4. Ant activity from 13 to 29 July in coffee bushes (eight total bushes) adjacent to an *Inga* in which *Azteca* was excluded from tending canopy scales (*Octolecanium*). Solid dots represent activity before exclusion and open dots represent activity before exclusion. Ants were excluded after measuring activity on the 16 July. Points represent number of ants per minute per bush. The regression line is fitted only to the postexclusion data points ($Y = -1.05 + 0.09X$, $r^2 = 19\%$). Not all dates are represented as some counts were cancelled as a result of adverse weather or logistical constraints.

Results of exclusion experiments are suggestive of a mutualistic association between *Azteca* and *Octolecanium.* Both a significant decline in density and a significant increase in sooty mold cover occurred in aggregations of *Octolecanium* from which ants were excluded. Six exclusion samples saw an increase in fungal cover, and five experienced a decline of >10% in scale density ($n = 8$), whereas these numbers were one and one, respectively, for controls ($n = 7$). In comparison to initial values, scale density decreased by a mean of 43.3% in exclusions, whereas sooty mold cover increased by a mean of value of 40.3% (Figs. 5 and 6). Control experiments saw an increase of 1.2% in sooty mold cover and a density decrease of 7.7%. The ant exclusion treatment had a significant overall effect on both relative density (one-way ANOVA, $P < 0.05$) and fungal cover ($P < 0.01$). Time since exclusion was significantly negatively correlated with density in both exclusion and control samples ($P < 0.01$ and $P < 0.05$, respectively). However, sooty mold cover increased significantly with time only in exclusions and not control samples ($P < 0.01$ and $P = 0.723$, respectively).

Discussion

Our results showed that there is a clear pattern of significantly reduced *C. viridis* density when *Azteca* nests in *Inga* compared with *Alchornea.* The high similarity of mean *C. viridis* density beneath *Inga* of 14.97 with that

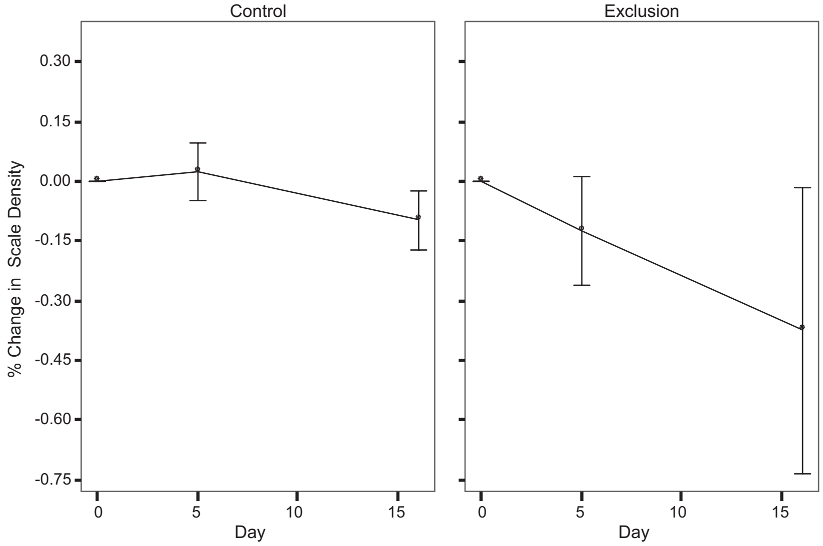

Fig. 5. Mean percent change in *Octolecanium* density from the previous sampling date in exclusion and control samples. Days 0, 5, and 16 represent 16 July, 21 July, and 1 August, respectively. Day 0 shows no change in both exclusion and control samples because it is the initial sample. Error bars represent 95% CIs.

in areas without *Azteca* of 14.29 suggests that the presence of *Octolecanium* aggregations in *Inga* effectively eliminates the *Azteca*–*Coccus* mutualism. The observed patterns of ant activity in the coffee layer support our hypothesis that competition for ant attendance is occurring between *C. viridis* and *Octolecanium* and suggest that a reduction in ant activity in coffee beneath *Inga* is the mechanistic driver. The preferential response shown by *Azteca* to *Octolecanium* indicates this scale species likely represents a more profitable honeydew resource. Although no direct test of honeydew quality or output volume was undertaken here, some studies have shown a positive relationship between body size and these variables in hemipterans (Mittler 1958, Hertel and Kunkel 1977, Costa et al. 1999). Thus, the larger body size of *Octolecanium* (Kondo et al. 2005) relative to *C. viridis* (Fredrick 1948) may result in differential attractiveness of honeydew to foraging workers. In addition, the absence of scale species in the canopy of 77% of surveyed *Alchornea* trees, the high density of *C. viridis* near nests in *Yucca,* and the increase in ant activity in coffee bushes after exclusion from an *Inga* canopy provides further support to our hypothesis.

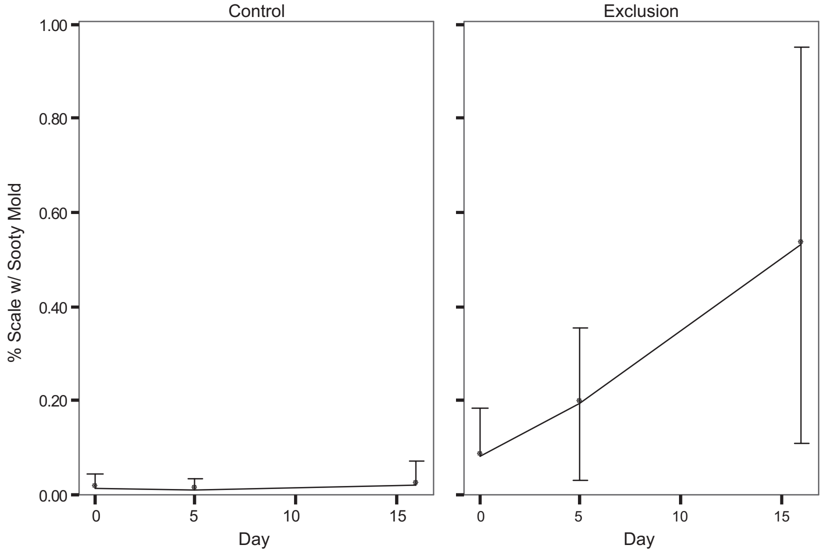

Fig. 6. Mean percent of *Octolecanium* individuals with sooty mold as a function of time since ant exclusion in exclusion and control samples. Day 0, 5, and 16 represent 16 July, 21 July, and 1 August, respectively. Error bars represent 95% CIs.

The observed decline in *Octolecanium* density after ant exclusion is consistent with many other studies of ant–hemipteran interactions and suggests a mutualism is occurring (Jutsum et al. 1981, Bristow 1984, Grant and Moran 1986, Bach 1991). In our system, the short-term declines observed were likely to have been a result of predation by coccinelid beetles and wasps (G.L., A.W., and C.K., unpublished data). The 40% average increase in *Octolecanium* scales with sooty mold is similar to increases seen in sooty mold cover on host plant leaves after ant exclusion from *C. viridis* aggregations in Hawaii (Bach 1991). Increases in sooty mold may also have contributed to scale mortality because it has been shown to affect crawler settling (Bess 1958) and adult mortality (Way 1954, Das 1959).

Interactions between aphids mediated by competitive hierarchies in ant attendance based on honeydew excretion quality and volume have been well documented (Fischer et al. 2001). In particular, our results are congruent with a study conducted by Cushman and Addicott (1991), which reported that the presence of conifer aphids (*Cinara* sp.) on spruce, *Picea engelmanni,* reduced the numbers of ant workers attending another aphid species (*Aphis varians*) on an adjacent herbaceous plant (*Epilobium angustifolium*). Aphid species in that system showed negatively affected fitness and abundance at lowered levels of ant activity (Cushman and Addicott 1989). However, determining whether the mechanism underlying this pattern is in fact indirect competition requires considering how variability in *Azteca* nest size, extrafloral nectaries in *Inga,* apparent competition between scale insects, and fungal pathogens of scales may influence our results.

Assessing ant abundance in *Azteca* nests is difficult because of the existence of satellite colonies and the logistical difficulty in counting ants that nest inside the truck on relatively large trees. However, the long-term survivorship of *Azteca* nests is higher in trees of larger circumference (such as *Alchornea*) and lower in *Inga* (J. Vandermeer and I. Perfecto, unpublished data). Thus, it is possible that nests of large size in *Alchornea* and small size in *Inga* resulted in our observed deviations from the expected pattern of canopy scale occurrence (three trees with scales in *Alchornea* and two without in *Inga*). Sudd and Sudd (1983) noted that ants may be less selective during times of high honeydew demand. High and low honeydew demand in *Alchornea* and *Inga* based on nest size, respectively, may be a determinant of *Azteca* selectivity and the tending of hemipterans that may be of lower quality. In *Inga,* EFNs could also be a sufficient carbohydrate source to eliminate the need to tend scales during times of low honeydew demand. However, experimental testing using membracids has shown that ants do not abandon honeydew-producing hemipterans in favor of EFNs (Del-Claro and Oliveira, 1993).

Other possible factors determining *C. viridis* density are not well supported. A coccinelid beetle, *Azya orbigera* Mulsant, is a shared predator among scale species in this system. This species shows a marked preference for feeding on *C. viridis* (G.L., unpublished data). Thus, there is potential for indirect interactions between scales through this predator adjacent to *Azteca* nests in *Inga.* These interactions, however, seem unlikely because neither adult or larval beetles are found in higher abundance in coffee bushes near nests in *Inga* compared with *Alchornea* (H. Liere, personal communication). In addition, a fungal pathogen, *Verticillium lecanii,* has been seen to devastate populations of *C. viridis* during the wet season (D. Jackson, personal communication). However, there is no reason to believe this fungus should preferentially attack *C. viridis* populations near *Inga.* Studies of the large-scale spatial and temporal factors affecting interactions between hemipteran species (i.e., dispersal and seasonality) are lacking and their importance here is unknown.

Patterns in *C. viridis* density at the study site are dependent at a primary level on the distribution of nests of *Azteca* (Vandermeer and Perfecto 2006). Secondarily, this abundance is determined by the biotic context of nest tree species. This dependence of a mutualism on the biological context in which it occurs has been observed in several other ant–hemipteran systems (Cushman and Addicott 1989, Fischer et al. 2001). However, unique to this system is the potential practical importance of these results and the persistence of context-dependent mutualism in a managed system. Although *C. viridis* usually does not attain pest status (Young 1982), previous work by Perfecto and Vandermeer (2006) has shown that an important agricultural pest of coffee, the coffee berry borer, *Hypothenemus hampei* Ferrari, may be partially controlled as a result of the *Azteca–Coccus* mutualism at this site. This study shows that the species composition of the shade tree canopy indirectly influences *C. viridis* density in the coffee layer. As shade tree diversity may be coupled with diverse ant–hemipteran associations, the potential pest management use of tree diversity merits future study.

Acknowledgments

We thank I. Perfecto, J. Vandermeer, H. Liere, T. Kondo, and D. Jackson and one anonymous reviewer for many helpful comments that greatly improved this manuscript. S. M. Philpott provided field assistance with collecting ant activity data. We also thank T. Kondo and J. Martin for assistance with identification of specimens. The generosity of the Peters family allowed this work to be conducted on their farm. G. L. Bautista helped to locate study sites and provided logistical support. This study was supported by NSF Grant DEB 0349388 to I.P. and J.V. Voucher specimens have been deposited at the University of California-Davis.

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Received 8 September 2007; accepted 6 March 2008.