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Effect of Disease Resistance on Secondary Herbivores: Aphid Abundance on Hybrid and Non-hybrid Coffee Varieties in the Chagga Homegardens

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Abstract

Coffee accounts for over 20% of Tanzania's income from foreign exchange and has been identified as an essential crop for the future of food security in Africa. Coffee production in the Kilimanjaro region, one of Tanzania's most important coffee-producing areas, is facing threats due to declining coffee prices, climate change, and outbreaks of fungal disease. Fungal-resistant hybrid coffee varieties have the potential to increase productivity and yields, although the ecological impact of their widespread introduction has not yet been determined. This study estimates the differences in aphid abundance and probability of aphid presence on hybrid and non-hybrid coffee plants in the Chagga homegardens. For this study, 1,119 coffee plants were sampled in 45 farms across 3 villages in the Kilimanjaro region. Hybrid coffee plants were 74.7% less likely to have the fungal disease coffee leaf rust (CLR) than non-hybrid plants ($p<0.001$). However, hybrid status was not found to be a significant factor in predicting aphid presence ($p=0.88$) or abundance ($p=0.71$). Factors that were significant in predicting aphid abundance included farm size ($p<0.001$), insecticide use ($p<0.001$), village ($p=0.001$), and ant count ($p<0.001$). The results of this study suggest that hybrid coffee has no significant bottom-up effect on the dynamics of the Chagga homegarden ecosystem.

Keywords: Aphids; Coffee; Chagga homegardens; Diseases secondary herbivores

Introduction

The Chagga agro-ecosystem is complex, consisting of multistory homegardens that are heavily intercropped to make efficient use of vertical as well as horizontal space. The primary crops grown in the Chagga homegardens are banana and coffee; other crops include maize, mangoes, avocadoes, yams, pumpkins, peas and papaya. While the Chagga homegardens are vital to Tanzania's economy, their ecological significance is not well understood. The coffee industry is an essential component of Tanzania's economy and the future of African development. The Inter-Academy Council (IAC) has identified coffee as one of the cash crops capable of improving food security and alleviating poverty in Africa [1]. By 2005, coffee was responsible for over 20% of the Tanzania's income from foreign exchange, with over 95% of farming families in Tanzania depending on coffee as their main source of income [2]. Moreover, an additional 2,000,000 people in Tanzania are employed either directly or indirectly by the coffee industry [2]. Kilimanjaro is one of three main coffee-producing regions, the other two being Mbeya and Matengo. The coffee grown on Kilimanjaro is primarily Arabica spp., the highest-selling coffee on the international market [3]. Kilimanjaro coffee also has added commercial value because of the romantic appeal of its geographic origin [4].

Several issues are currently threatening coffee production in Tanzania. Farmers are losing interest in selling coffee due to both ecological and economic considerations. These include receiving a low share of coffee prices, lack of predictable rainfall due to climate change, and decreasing productivity of coffee plants. Of all these factors, the decreases in productivity have been attributed to increasing plant age and insufficient pruning and pest/disease management. The two varieties of Arabica grown in Tanzania are Kent and Bourbon, both of which are highly susceptible to two fungal diseases: coffee berry disease (CBD) and coffee leaf rust (CLR). Both CBD and CLR can affect coffee bean production if left untreated. CBD directly affects the coffee berries and causes the beans to stop developing properly; CLR primarily affects the leaves of the coffee plant thereby decreasing photosynthetic potential.

The Tanzania Coffee Research Institute (TaCRI) has been working for the past 13 years to develop hybrid varieties of Arabica coffee that are resistant to both CBD and CLR. In addition to disease resistance, TaCRI hybrid coffee varieties have higher yields and better beverage cup quality than non-hybrid varieties. To date, TaCRI has released 15 hybrid varieties of Arabica coffee. Hybrid varieties are developed by selectively crossing the Kent and Borbon varieties with other coffee varieties from outside of Tanzania that possess desired traits for disease resistance and good cup quality. The hybrid coffee varieties most commonly grown on Kilimanjaro are N39 varieties, which are of Bourbon origin. These hybrids are marketed as having resistance to both CBD and CLR [5].

Hybrid coffee varieties resistant to CLR and CBD represents a rapidly growing proportion of the coffee, grown in Chagga homegardens of Kilimanjaro [5]. The purpose of this study was to evaluate the ecological effects of introduced hybrid coffee varieties on secondary herbivores. Specifically, how does inbred resistance to fungal disease affect aphid abundance on hybrid coffee plants in the Chagga homegardens, an ecologically and economically important farming system? Other factors that were considered include intercropping

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pattern, farm size, farm location, crop biodiversity, and shade tree species. Results were analyzed using descriptive statistics and proportional odds logistic regression. We expected aphid abundance to be higher on fungal-resistant hybrid plants and on non-hybrid plants in close proximity to improved lines.

Study species

The black citrus aphid *Toxoptera aurantii* has been observed on 5 continents and has a large host plant range that includes many economically important crop species. *T. aurantii* infests only the inflorescences, buds, and young leaf parts of its host plant [6,7]. *T. aurantii* is tended by the ant species *Camponotus acvapimensis*, which farms the aphid to collect its sugary waste product, honeydew, as a food source. An alteration in the abundance of secondary herbivores such as *T. aurantii* could have direct bottom-up ecosystem-wide effects by affecting the levels of ants, insect predators such as the syrphid flies, and plant damage by other herbivores [8,9]. A study of cocoa plants in Ghana showed that syrphid abundance correlates positively with aphid abundance [10]. Conspecific plants experience differences in herbivore susceptibility due to variations in phenological, morphological and chemical defense traits [11]. It is therefore possible that the altered morphology and heightened defense response of introduced hybrid coffee varieties could affect herbivore feeding behavior.

Study site description

This study was conducted in the Kilimanjaro region of Tanzania in the villages of Lyamungu, Kibosho-Mweka, and Sembeti (Figure 1). Kilimanjaro is situated between 3º14'42.96"S and 37º19'44.66" E, map of study site was generated by using data from GPS unit and Google Earth. The altitudes of the villages surveyed are 1273, 1311, and 1187 meters above sea level, respectively. Average annual rainfall ranges from 1,000 to 2,000 millimeters. The climate in this region is tropical montane with two rainy seasons: long rains from March-May and short rains from November-December. The Kilimanjaro region occupies mountainous slopes that have aspects ranging from south to southeast and grades between 16-60% [12]. In total, the region is about 13,209 square kilometers [13].

According to a 2012 census, the population of the Kilimanjaro region is 1,640,087, a 1.8% increase since 2002. The population density is about 650 people per square kilometer. The average amount of land per household is between 1 and 2 hectares and the average number of people per household is 4.3 [12,14]. The average size of the farms we surveyed was 0.23 hectares (ha). The largest farm was 1.0 ha and the smallest farm was 0.045 ha.

Figure 1: Study site locations on Mount Kilimanjaro. Triangles represent farms visited (15 per village).

The Wachagga are a Bantu people who were originally immigrants of numerous groups that once settled on the foothills of Mt. Kilimanjaro about 300 years ago [15]. *Coffee arabica* was introduced as a cash crop to Kilimanjaro about 100 years ago [2].

Methods

The sample frame for this study was small-scale Chagga farms that grow coffee on Kilimanjaro. The sample population drew from a random sampling of farms that have and have not adopted hybrid coffee varieties in the villages of Kibosho-Mweka, Lyamungu, and Sembeti. Lyamungu and Kibosho were chosen because they have high rates of adoption of the hybrid coffee varieties due to their proximity to the Tanzania Coffee Research Institute [5]. Sembeti has a lower rate of adoption, due to a complex array of historical and economic factors. Twenty five coffee plants were measured on each farm. Coffee plants were chosen by randomly selecting 5 rows of coffee and 5 positions within each row. In total, we visited 45 farms, and surveyed 1,119 coffee plants. Of the plants sampled, 509 were hybrids and 610 were non-hybrids.

Four measurements were taken from each coffee plant: presence/absence of CLR, number of aphids on the plant, number of ants on the plant, percent of leaves browsed, and distance to the nearest hybrid. CLR presents as rust-colored spots on the underside of the leaves, with defoliation occurring in advanced stages of the disease. Aphid abundance per plant was recorded and later grouped into categories of 0, 1-10, and >10. Approximate number of ants on the entire plant was also noted. An exact count was given for plants with fewer than 50 ants. For plants with over 50 ants, the number of ants was approximated by the following categories: 50-99, 100-199, 200-299, 300-399, 400-499, and >500. To measure leaf browsing, a random branch on each plant was selected and the ratio of browsed leaves to total leaves on the branch was recorded.

We also collected data on homegarden characteristics. The area and GPS coordinates of the cultivated land were measured for each farm using a Garmin Dakota 20 GPS unit. Species richness of all cultivated crops and shade tree species was determined by both visual observation and survey results. We recorded intercropping pattern (banana or banana-maize) by noting which crop species, if any, were planted with the coffee.

Chagga farmers were surveyed to obtain data on farming practices and pest management. Survey results were analyzed using descriptive statistics. Field data were analyzed using binary logistic regression and proportional odds logistic regression in the MASS package of R [16]. Likelihood ratio tests were used to assess the effect of coffee variety on aphid abundance.

Results

Incidence of disease

The incidence of disease differed significantly between the hybrid and non-hybrid coffee plants that were surveyed for the presence/absence of CLR (GLM: Likelihood ratio=67.73, Test df=1, $p<0.001$). Fifty nine percent (n=303/509) of the hybrid plants under study had CLR, while 88.2% (n=538/610) of the non-hybrid coffee plants were affected (Figure 2). All other variables held constant, the odds of a hybrid coffee plant having CLR are 0.26 times the odds for non-hybrid coffee plants. Farm size, village, cropping pattern, and fungicide use were also significant factors in accounting for the presence of coffee leaf rust. Fungicide use was no longer significant in a model that also

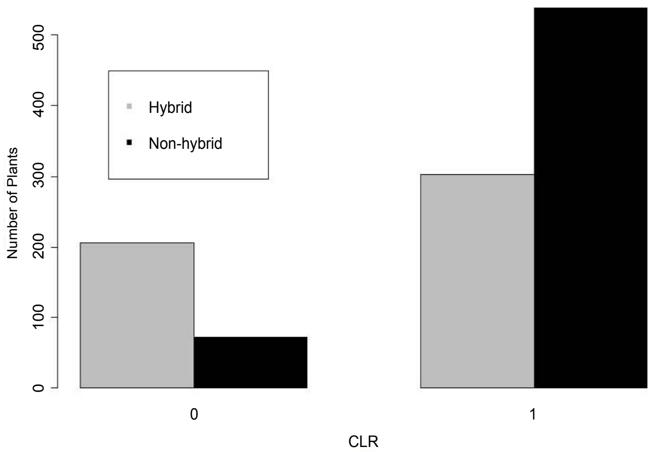

Figure 2: The incidence of coffee leaf rust on hybrid and non-hybrid coffee varieties in the Kilimanjaro region.

	Odds ratio	S.E.	Pr(>|z|)
β0	0.295	0.288	2.37E-14
β1	0.904	0.1733	0.560
β2	1.745	0.192	0.002
β3	0.998	0.001	0.004
β4	1.345	0.089	<0.001
β5	2.022	0.224	0.003

S.E: Standard error of the model coefficients.

Table 1: Odds ratios derived from the coefficients of a generalized linear model predicting the presence/ absence of aphids on coffee plants in the Kilimanjaro region.

accounted for hybrid status (p=0.861). Fifty eight percent (n=116/200) of the plants grown on farms that did not apply fungicide were disease-resistant hybrids.

Aphid occurrence

The presence or absence of aphids on a coffee plant did not differ significantly among hybrid and non-hybrid coffee plants (GLM: Likelihood ratio=(-0.02), Test df=1, p=0.88). A binary logistic model in which is the estimate for the probability of aphid presence is given by equation.

$$\log(\pi/-\pi)=\beta_0+\beta_1(\text{Lyamungo})+\beta_2(\text{Sembeti})+\beta_3(\text{ants})+\beta_4(\log(\text{hectares}))+\beta_5(\text{insecticide})$$

Village, farm size, application of insecticide, and approximate number of ants were found to be significant predictors of aphid presence (Table 1). A model that incorporates the above variables fits significantly better than an empty model with no predictors (Likelihood Ratio=38.88, Test df=5, p<0.001)

Insecticide use resulted in an increase in the odds of finding aphids on a coffee plant by a factor of 2.0. A 10% increase in farm size is accompanied by a 12% increase in the odds of aphid presence. Ants were also frequently found on plants which harbored aphids, although the relative number of ants did not drastically alter the odds of aphid presence (Table 1).

Aphid abundance

Proportional odds logistic regression was used to assess whether hybrid status influenced aphid loads on coffee plants. Aphid population size did not differ significantly among hybrid and non-hybrid coffee plants after accounting for village, ant count, farm size, and insecticide use (POLR: Likelihood ratio=0.136, Test df=1, p=0.712). For the purposes of POLR, aphid number was grouped into ordered categories of 0, 1-10, and >10. All other variables held constant, a 10% increase in farm size resulted in a 12.8% increase in the odds of a one unit increase in aphid abundance (i.e., the odds of aphid number moving from 0 to 1-10 or from 1-10 to >10). Likewise, the odds of an increase in aphid abundance were 2.1 times as great in farms that used insecticide compared to farms that did not, all other variables held constant (Table 2). Although ant count was a significant term in the model, an increase in ant count had a marginal effect on aphid loads. Compared to Kibosho, the odds of an increase in aphid numbers on coffee plants were 78% higher in Sembeti.

Survey results

Farmers were asked to describe their methods of controlling disease and insect pests on coffee. They were asked to provide the name and amount of chemicals applied to coffee plants on their homegardens. Seventy seven (35/45) of the respondents used both insecticide and fungicide to control harmful insects and disease. Eighty two percent (37/45) of farms applied fungicide, while 94.6% (35/37) also applied insecticide. Survey results are summarized in Table 3.

Farmers that did not apply either fungicide or insecticide to their crop cited the prohibitive cost of chemical remedies as their primary reason for doing so. Thirty nine per cent (18/45) of the farmers surveyed claimed to employ non-chemical measures to control insects on coffee in addition to applying insecticide. Of these, 61.1% (11/18) applied engine oil on the stems of coffee plants to reduce coffee borer populations. Additional non-chemical remedies to alleviate pest problems included application of banana beer residue to trap ants, farm cleanliness, and planting after fallow periods.

Discussion

Aphid abundance on hybrid coffee

The results of our study indicate that there is no reason to believe

	Odds ratio	S. E.	p-value
Lyamungo	0.924	0.171	0.645
Sembeti	1.780	0.190	0.002
Ants	0.998	0.001	0.001
Log(Hectares)	1.338	0.088	0.001
Insecticide	2.080	0.222	0.001

Table 2: Odds ratios for a POLR modeling the effect of village, ant count, farm size, and insecticide use.

Insecticide	**Farmers that apply (%)**	**Average amount applied/year (ml)**
Dursan	77.8	589.4
Thionex 35C	11.1	292.5
Celecron	8.9	600
None	17.8	0
Fungicide	**Farmers that apply (%)**	**Average amount applied/year (kg)**
Blue copper	82.2	3.5
Red copper	8.9	3.7
None	17.8	0
Method of pest control	**Farmers that apply (%)**	
Insecticide	82.2	
Fungicide	82.2	
Other measures	40.0	
None	4.4	

Table 3: Summary of survey data.

that the introduction of disease-resistant hybrid coffee plants in the Chagga homegardens has an effect on the abundance of *T. aurantii* (Figure 3). As such, it is also unlikely that there are any additional bottom-up effects on the ecosystem level, although further research is necessary to clarify this point.

Our study did not differentiate among the multiple varieties of improved coffee lines grown in the Chagga homegardens, the inclusion of which may have yielded more significant results. A future study that takes specific varieties into account may be able to evaluate differences in aphid loads on plants that share common genetic markers for disease resistance. Additionally, many of the hybrid plants surveyed were not distributed by the Tanzania Coffee Research Institute. Many Chagga coffee-growers cultivate a Brazilian variety of Arabica that is derived from crosses involving Hibrido de Timor (HT), a CLR-resistant line that was developed in the late 1950s. HT and HT-derived progeny lack resistance to CBD, unlike the hybrids that TaCRI distributes, which display resistance to both fungal diseases [17]. Thus, it is possible that the hybrids we surveyed did not share common defensive responses to fungal disease, which could have influenced the significance of the hybrid term in the regression analyses.

Village

Farm location (village) significantly affected the presence and relative abundance of *T. aurantii* on coffee plants. Cropping pattern was not a significant variable in a model that also included the village term (GLM: Likelihood ratio=(-0.41), Test df=1, p=0.53). Each village we visited tended to make nearly exclusive use of either one type of cropping pattern or the other (Figure 4). For instance, 100% of the farms we sampled in Sembeti grew coffee intercropped with banana, while 83.2% (12/15) of the farms sampled in Kibosho grew coffee that was intercropped with both banana and maize.

In addition, aphid abundance on coffee plants intercropped with both banana and maize tended to be lower than aphid abundance on coffee plants intercropped with banana alone. It has been suggested that the abundance of natural enemies of herbivores increases with greater crop biodiversity [18]. By extension, higher natural enemy species richness is strongly associated with a reduction in herbivore abundance [19]. Polycultures promote greater diversity and abundance of generalist predators by supporting a greater array of herbivores throughout different stages of the growing season [18]. The association

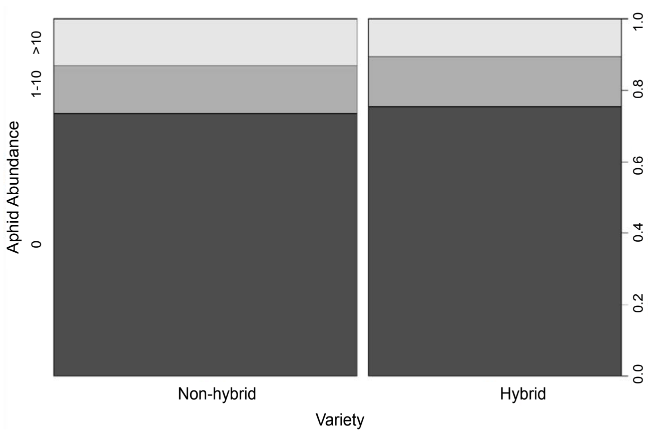

Figure 3: Percent of hybrid and non-hybrid coffee plants with varying aphid loads. There is no significant difference in aphid loads among hybrid and non-hybrid coffee plants in the Kilimanjaro region, n=1119 coffee plants.

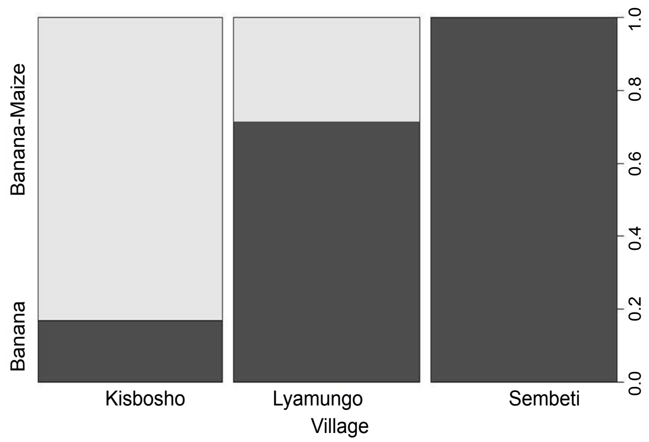

Figure 4: Percent cropping pattern by village in the Kilimanjaro region. Graph generated in R.

between villages and cropping pattern, and the effect of cropping pattern on aphid abundance thus suggests that maize may play a role in supporting generalist predators that feed on *T. aurantii*.

The village term also encapsulates a large array of geographical and meteorological variation in farm location that was not captured in the data. It is the inclusion of this amount of extra variation that could explain why cropping pattern is not significant in a model that also includes village. It is currently unknown whether altitude affects the distribution of *T. aurantii*, although the villages surveyed shared such similar altitudes that it is unlikely that it would have a significant effect. However, previous research has demonstrated that peaks in the population of *T. aurantii* track peaks in rainfall [10]. It is thus likely that variations in regional rainfall may play some role in the regulation of aphid and predator abundance (Appendix 1).

Farm size

Plants on larger farms had a greater probability of having larger aphid loads. Farm size and crop species richness were collinear; farm size accounted for 20.7% of the observed variation in crop species richness. A 10% increase in farm size was accompanied by an increase of 0.10 in expected mean crop species richness (Figure 5). As noted previously, crop species richness has been linked to more stable herbivore populations by providing a greater number of possible host plants and microhabitats. It is also likely that farm perimeter-to-area ratio plays a role in influencing herbivore behavior [18]. This study supports the theory that farms with a lower perimeter-to-area ratio have larger aphid populations, although there is currently a lack of evidence in the literature to support this observation.

Ant abundance

Ant abundance is a significant factor in predicting aphid abundance on both hybrid and non-hybrid coffee plants, though an increase in ant abundance corresponded with a negligible change in aphid abundance. There are several possible explanations that could account for the observed relationship between ant and aphid abundances. *T. aurantii* are often found with the ant species that tends them, *C. acvapimensis*; one would thus expect to observe a strong positive relationship in the populations of these two species. Our study, however, did not differentiate among ant species that tend other hemiptera. *Pheidole megacephala* tends the green scale insect that feeds on young shoots

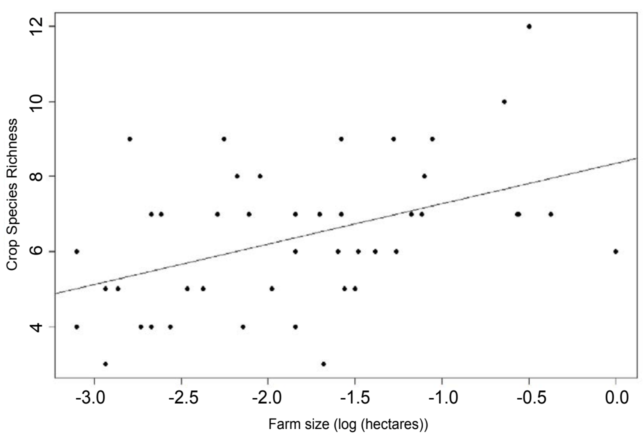

Figure 5: Effect of farm size on crop species richness. The relationship between crop species richness and farm size is moderately linear (R^2=0.207).

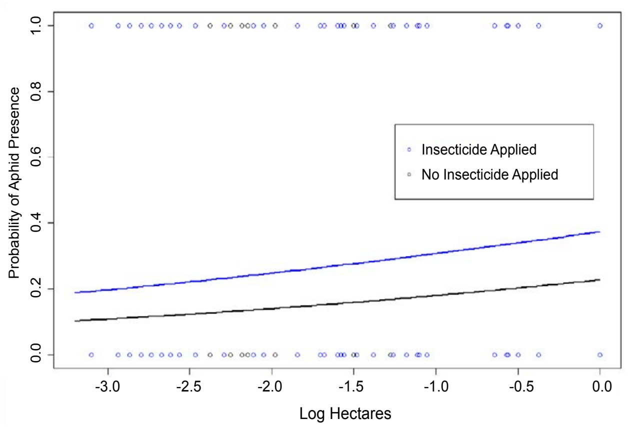

Figure 6: Effect of insecticide application on aphid presence. Insecticide application resulted in a higher probability of aphid presence that increased with farm size.

of the coffee plant [20,21]. The presence of coffee green scale was often accompanied by large numbers of *P. megacephala*, a confounding variable that was not accounted for in the data. From what we observed, *T. aurantii* was seldom present on a coffee plant with a major green scale infestation. Nevertheless, the fact that ant abundance is significant in predicting aphid loads suggests that a change in aphid abundance likely influences ant presence on coffee plants, regardless of species.

Insecticide use

The odds of an increase in aphid abundance were 2.0 times higher on farms that used insecticide than on farms that did not. As is shown in Figure 6, the probability of aphid presence was higher across all farm sizes on plants that had been treated with insecticide than on plants that had not been treated. Insecticide use has been shown to increase aphid abundance in other agriculture systems. A study of the effects of insecticide on potato plants found that aphid abundance was 28 times higher on treated plants than untreated plants after insecticide application [22]. One explanation for this result is that insecticide use decreases abundance of natural aphid predators, which in turn increases aphid levels. Non-selective insecticides can target aphid predators without killing the aphids themselves [23].

Most importantly, however, is that insecticide use leads to an increase in aphid tending ant species. Application of insecticide has been found to lead to higher abundances of ground-nesting ants, which tend many species of sap-sucking hemiptera [24]. Based on our results, it is highly likely that the use of insecticide on coffee increases the population of *C. acvapimensis*, the ground-nesting ant species that tends *T. aurantii*.

Limitations and Recommendations

Several observational biases could have affected the outcome of the study. First, plants that have CBD and plants that have a large infestation of *Coccus viridis* (also known as coffee green scale) produce visually similar symptoms. Where CBD causes black lesions on the berries and stem of coffee plants, coffee green scale produces a black, sooty mold. It is difficult for a non-expert to differentiate between these two problems; for some plants in this study, coffee green scale infestations may have been mistaken for CBD, and vice versa. Because of the potential for inaccuracy in CBD identification, CBD measurements were not considered in the statistical analysis. Second, we did not take the species of ant present on the coffee plant into account. Thus, we cannot draw any conclusions about the relationship between the abundances of *T. aurantii* and that of specific ant species. Third, the farms that we visited were not evenly distributed geographically within the villages, and a number of farms that were studied share a border.

This study was limited by three factors that were difficult to control for. First, the time of year is highly relevant to aphid abundance. In Ghana, the abundance of *T. aurantii* on cocoa plants has been found to peak five times per year in accordance with the rainy seasons [10]. This study was conducted in the first two weeks of November, before the start of the short rainy season; aphid numbers were likely still recovering from the dry season, which explains why aphids were absent from the majority of plants surveyed. Second, recent spraying of insecticide on farms was not considered in data analysis because the variation in insecticide type, amount, and spray date was too great to consistently account for. Finally, hybrid and non-hybrid coffee plants are indistinguishable by appearance alone. Hybrid and non-hybrid plants were differentiated based on age and location on the farm, with no method by which to definitively confirm plant identity.

The results of this study suggest multiple opportunities for future research. The development of microsatellites would provide a way to definitively distinguish between Brazilian hybrid varieties, TaCRI hybrid plants, and non-hybrid plants. This study could be conducted at different times of year and in more villages in the Kilimanjaro region in order to capture more variation in climate, elevation, and weather. Geographical and meteorological data could also be recorded for each village and included in the analysis. Another direction of interest could be to compare the elemental composition of the leaves of hybrid and non-hybrid coffee to investigate its relationship to aphid and ant abundance on both varieties. Elemental composition of the purple coneflower *Echinacea angustifolia* has been shown to influence aphid and ant levels in the North American prairie [25]. It would be also be valuable to identify differences in secondary compounds between hybrids and non-hybrids, and determine whether these differences relate to herbivore abundance. Finally, the fitness of F1 crosses between hybrids and non-hybrids could be studied to assess the possible long-term ecological effects of the introduction of hybrid coffee in the Chagga homegardens.

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