

Local and Landscape Constraints on Coffee Leafhopper (Hemiptera: Cicadellidae) Diversity

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Abstract

The intensification of agriculture drives many ecological and environmental consequences including impacts on crop pest populations and communities. These changes are manifested at multiple scales including small-scale management practices and changes to the composition of land-use types in the surrounding landscape. In this study, we sought to examine the influence of local and landscape-scale agricultural factors on a leafhopper herbivore community in Mexican coffee plantations. We sampled leafhopper (Hemiptera: Cicadellidae) diversity in 38 sites from 9 coffee plantations of the Soconusco region of Chiapas, Mexico. While local management factors such as coffee density, branches per coffee bush, tree species, and density were not important in explaining leafhopper abundance and richness, shade management at the landscape level and elevation significantly affected leafhoppers. Specifically, the percentage of low-shade coffee in the landscape (1,000-m radius surrounding sites) increased total leafhopper abundance. In addition, Shannon's diversity of leafhoppers was increased with coffee density. Our results show that abundance and diversity of leafhoppers are greater in simplified landscapes, thereby suggesting that these landscapes will have higher pest pressure and may be more at-risk for diseases vectored by these species in an economically important crop.

Key words: disease vectors, herbivore, landscape scale, leafhoppers, shade management

Agricultural intensification has resulted in numerous environmental problems including the loss of biodiversity and ecosystem services (Matson et al. 1997, Tilman et al. 2001, Foley et al. 2005, Philpott et al. 2008a, Flynn et al. 2009). The addition of chemical pesticides, removal of native plant species, a shift from polycultures to monocultures, and the increasing size of agricultural fields make it increasingly difficult for many species to maintain stable populations in these agroecosystems (Vandermeer et al. 1998, Tscharntke et al. 2005). In addition, the frequent, intense disturbances of crop fields by machinery prevent insect species from gaining footholds in available niches (Landis and Marino 1999).

The species found within agricultural fields are a product of the regional species pool within the surrounding landscape. For example, habitat features in adjacent uncultivated fields such as hedgerows, fallows, or forest fragments aid in the maintenance of some populations within fields (Tscharntke et al. 2005). This is likely because these habitat features provide refuge for insects that move between cultivated and adjacent uncultivated areas during application of pesticides, harvest, and other management practices that

cause direct insect mortality (Wissinger 1997). Other management techniques, such as increased crop diversity or polycultures may reduce herbivore pressure, increase the abundance of natural enemies, and reduce pest damage when compared with simplified monocultures (Letourneau et al. 2011). Less intensive management or diversified agricultural practices can promote in-field biodiversity of beneficial and non-beneficial species (Vandermeer et al. 1998, Tscharntke et al. 2005).

The response of herbivore communities to agricultural intensification is dynamic and inconclusive. Given the assumptions of the resource concentration hypothesis (RCH; Root 1973), pest abundance should increase where “resources” (i.e., crops) are concentrated, at the local or the landscape level. The “natural enemies hypothesis,” also proposed by Root (1973) predicts that pest populations will be lower in diversified agricultural managements as polycultures can attract and maintain a higher abundance and richness of natural enemies. At the same time, pest diversity may be higher in these diversified landscapes. This is because the natural enemies may suppress dominant herbivores and prevent them from

monopolizing the resources thereby allowing for more diverse herbivore assemblages. However, it is also possible that pest diversity increases with agricultural intensity, if pest diversity is facilitated by crop productivity (Siemann 1998, Bianchi et al. 2006). A recent meta-analysis found support for some of these hypotheses, showing that farms within simplified landscapes (high proportion of cropland) had greater rates of pest population growth, but lower pest richness, and no clear pattern of pest abundance (Chaplin-Kramer et al. 2011) suggesting the need for more research in this area.

Coffee is among the most important global commodities and provides livelihoods to millions of people. It is traditionally grown under a canopy of shade trees, and can therefore provide good quality habitat for multiple species (Perfecto et al. 1996, Philpott et al. 2008a). However, in many coffee-growing regions intensification of coffee plantations has commenced and includes the reduction of shade trees. As a result, coffee plantations in the Neotropics vary substantially in shade tree density, shade tree diversity, and canopy complexity (Moguel and Toledo 1999), which have had differing effects on different taxonomic groups. In addition to local level shade factors, the surrounding landscape around coffee plantations is important to the species found within coffee farms. For example, nearby forest species provide “spill over” effects that contribute to improved pollination and pest-control services (Ricketts et al. 2004, Karp et al. 2013). Landscape heterogeneity may also be important for species living within coffee plantations that require multiple habitat types to maintain viable populations in plantations (Tschardt et al. 2005).

Although various taxonomic groups have been investigated with regards to effects of local management or landscape factors on them, few have studied how leafhoppers respond to both local and landscape management level effects simultaneously. Leafhoppers (Hemiptera: Cicadellidae) use sucking mouthparts to siphon fluids from the xylem of plants (Mattson 1980). While leafhoppers are not thought to cause severe damage to coffee plants through herbivory, they can transmit plant pathogens such as the bacterium *Xylella fastidiosa*, a pathogen linked to the coffee leaf scorch and crespita disease in Brazil and Costa Rica, respectively (Beretta et al. 1996, Li et al. 2001, Rodríguez et al. 2001, Redak et al. 2004). To better understand how to control these herbivorous pests and their associated diseases, it is necessary to first study the factors that contribute to the distribution and abundance of leafhoppers. Previous work from coffee plantations in Costa Rica suggests that leafhopper abundance declines with shade and increases with more surrounding forests fragments (Ramos 2008). Another study of leafhoppers in Mexico shows that the composition of shade tree species is important to their abundance and richness, however in this case landscape characteristics were not investigated (Burdine et al. 2014).

The purpose of this study was to determine which local and landscape factors contribute to the richness and total abundance of leafhoppers in Mexican coffee plantations. Following the resource concentration and the natural enemies hypotheses (Root 1973), we predicted that leafhopper abundance would increase with increasing local shade management intensity (decreasing shade tree density), and increase with the percentage of low-shade coffee land use in the surrounding landscape. We predicted leafhopper diversity would increase with an increase in the percentage of high shade coffee land use in the landscape.

Methods

We performed this study in the Soconusco region of Chiapas, Mexico across nine coffee plantations ranging from 600 to 1,300 m

above sea level (masl). The Soconusco region is largely dominated by coffee agriculture (94%) with small forest fragments mixed throughout the coffee matrix (6%) (Philpott et al. 2008b). We established 38 sites that differed in a number of local management and landscape level characteristics and established a minimum distance of at least 300 m between sites. These sites fell within nine large coffee plantations, ranging in size from 1000 to 6 ha, but most farms were ~300ha. We selected an intermediate distance (300 m) between sites so as to avoid extreme differences within a given farm while still having varied landscape-level factors between nearby sites.

At each site we measured a number of local factors related to management intensity. We used a GPS (Garmin GPSmap76CSx) to map an approximate 1-ha circle around each site and documented the abundance and richness of tree species >10 cm dbh within that area. An incidence-based coverage estimator in the program EstimateS (Colwell et al. 2012) was used to approximate the total number of tree species within a site. A prior study in the same area of Mexico revealed that leafhopper species respond to the density of *Inga* spp. trees (Burdine et al. 2014), therefore we calculated the percentage of *Inga* spp. per hectare in each plot. To estimate the density of coffee bushes, we established a 15 × 15 m sub-plot at the center of the 1-ha plot and counted all the coffee plants within the plot. We recorded shade cover using a convex spherical densiometer (Forestry Suppliers, Inc., Jackson, MS, USA) at three spots in each site, 5 m away from the center of the site at 0°, 120°, and 240°. In each of the three spots we measured the shade cover in all four cardinal directions. We also measured groundcover extent and groundcover species richness in five 0.5-m² quadrats set at 5 m from the plot center every 72°. Cover was estimated using the following ranges: 0–1, 2–5, 6–20, 21–40, 41–60, 61–80, and 81–100%.

To obtain landscape level factors at each sampling site, we used Geographic Information Systems (GIS) and measured landscape heterogeneity by digitizing the borders of forests and plantations of varying shade tree management intensity using a basemap in ArcGIS 10 (ESRI 2011). Plantation boundaries were used to define rough categorizations of landscape shade management intensity based on the average percent shade cover of plantations: high- (>70%), medium- (30–70%), and low- (<30%) shade management. Some plantations had large areas of more than one category of shade intensity level; therefore we delineated these areas and categorized each area into its appropriate level. For each site, we calculated percent forest, low-shade, medium-shade, and high-shade coffee land-use types within a 100, 250, 500, and 1,000 m radius surrounding each site. We also calculated the Shannon’s diversity index ($\Sigma -\ln(p)/p$) of the habitat types at these scales. The response of dependent variables to each landscape factor across these four scales were correlated (Supplementary material), therefore we proceeded with only the 1,000 m scale to maximize the differences between the local and landscape scales used in analysis. The means and ranges for all variables measured are listed in Table 1. We tested for spatial autocorrelation in our data using Mantel test of geographic distance among sites and abundance, richness, and Shannon’s diversity of leafhoppers. We found no significant correlations between geographic distance and abundance (Mantel $r = -0.1010$, $P = 0.963$; R ade4 package), richness (Mantel $r = -0.0897$, $P = 0.884$), and Shannon’s diversity (Mantel $r = -0.0640$, $P = 0.892$) of leafhoppers (Legendre and Legendre 1998).

Leafhoppers were collected by sweep netting 15 coffee bushes in transects on 2 occasions between May and July of 2012 between the hours of 7:00 and 14:00. Each bush received four upward sweeps of the net starting at the base of the bush and moving upward. In addition to sweep netting, we also sampled the leafhopper community

Table 1. Mean and range values of local and landscape factors

Management factors	Mean	Range
Local factors		
Coffee density (per 225 m ²)	74	21–154
Shade tree density (per ha)	173	63–337
Shade tree richness (estimated per ha)	29	10–73
<i>Inga</i> spp. in plot (%)	60	16–94
Herbaceous height	6.5	2.4–12.8
Herbaceous cover (%)	56.5	4–100
Herbaceous spp.	6	2–11
Landscape factors ^a		
High-shade coffee land-use (%)	28.4	0–84
Medium-shade coffee land-use (%)	37.2	0–96
Low-shade coffee land-use (%)	26.6	0–86
Forest (%)	7.7	0–18
Habitat diversity (Shannon's Index)	0.81	0.17–1.24
Other factors		
Elevation (masl)	942	595–1273

^aLandscape factors were measured at a 1000 m radius surrounding site centers.

by using pan-traps in the center of each site on one occasion per site. We placed two white, yellow, and blue pans (350 ml volume bowls) at the center of each plot. Three bowls, one of each color, were elevated ~15 cm above the ground surface and another three bowls were elevated 45 cm above the ground, using PVC piping. Pan-traps were filled with a water solution of salt and liquid Dawn dish soap. To make the solution, we mixed 2 kg of table salt and 80 ml of Dawn dish soap dissolved in 20 liters of water (as in [Burdine et al. 2014](#)). We opened pan-traps at ~8:00 and collected pan-traps at ~14:00, maintaining the same order so that all traps were open for roughly the same amount of time. We then combined the contents of all six pan-traps (per site) after sorting, rinsing, and storing contents in 70% alcohol. Each site was defined as a replicate, with individuals combined from the two sweep netting events and the pan trap sample. We later identified all individuals of the family Cicadellidae from both the sweep net and pan-trap sampling and assigned each individual to tribe within subfamilies and morphospecies based on morphological traits and the keys in [Wilson et al. \(2009\)](#), [Dmitriev \(2003\)](#), and [Nielson and Godoy \(1995\)](#). We constructed a species accumulation curve (MaoTao estimation) in the program Estimate S ([Colwell et al. 2012](#)) to determine if we had sampled sufficiently to capture the leafhopper community.

To determine the relative significance of local and landscape factors in explaining leafhopper diversity, we conducted multivariate analysis using generalized linear mixed models (GLMM). Due to a large number of independent variables and a large number of potential interactions between these independent variables, we first produced two smaller models, one with only local scale factors and another with only landscape scale factors before combining the most parsimonious model into a final local-landscape model (as in [Stenchly et al. 2011](#)). We tested for collinearity between independent variables via comparison of variance inflation factor (VIF; [Neter et al. 1996](#)) and considered a VIF above 3 as a factor that was strongly collinear. We removed the landscape factor “percent medium shade” and the local factor “percent herbaceous cover” from models because these significantly increased VIF and were thought to be ecologically insignificant or redundant with other factors. In all models, plantation was introduced as a random effect to account for unequal sample-size between plantations. Each landscape model considered percent forest, low shade coffee, high shade coffee, and

habitat diversity (Shannon's diversity) as independent variables (at 1000 m radii). Each local model considered herbaceous height, herbaceous richness, coffee density, shade tree density, estimated shade tree richness, and percent *Inga* tree spp. as independent variables. We performed model selection via comparison of Akaike Information Criteria corrected for sample size (AICc) and parameter number, keeping the most parsimonious models ([Burnham and Anderson 2002](#)). For the final local-landscape model, the most parsimonious model was selected using Δ AICc and all models with Δ AICc < 2 were examined and finally, we used model averaging to determine the importance of each independent variable ([Supplementary material](#)). We constructed local, landscape, and local-landscape models for the following leafhopper-dependent variables: total abundance, richness, and the abundance of the five most numerous leafhopper species (*Macugonalia redundans* [Fowler 1899], *Sibovia* sp., *Isogonalia* sp., *Agallia* sp. 1, and *Agallia* sp. 2). To correct for effects of density on richness and Shannon's diversity index, abundance was included as a covariate in models investigating variation in richness and in the Shannon's index. We tested for the normality of dependent variable distributions by comparing the residuals of the model with q–q plots and with Kolmogorov–Smirnov tests. Abundance and Shannon's diversity index followed normal distributions we therefore analyzed these variables with linear mixed effects models with the function ‘lme’ in the “NLME” package in the Program R (R 3.0.1) ([Pinheiro et al. 2016](#)). We checked for lack of homoscedasticity using the Breusch–Pagan test (Package `lmtest`). We analyzed all other dependent variables with GLMM assuming a Poisson distributed error distributions and log-link functions, with the function ‘glmer’ in the ‘lmer’ package ([Bolker et al. 2009](#)). We calculated marginal R^2 of the final models using the `r.squaredGLMM` function from the MuMIN package ([Bartoń 2013](#), [Nakagawa and Schielzeth 2013](#)).

Results

We found a total of 299 individuals of 38 morphospecies. Although the observed density was small, the estimated species accumulation curve approached asymptotic species richness for this coffee leafhopper community, suggesting our sampling had captured a significant portion of the leafhopper community (Fig. 1). Of the 38 morphospecies found, 5 species—*M. redundans*, *Sibovia* sp., *Isogonalia* sp., *Agallia* sp. 1, and *Agallia* sp. 2 ([Nielson and Godoy 1995](#))—made up ~37% (110 individuals) of total leafhopper abundance.

Results of the linear mixed effects models revealed that the proportion of low-shade coffee land-use was positively related to the abundance of leafhoppers ($R^2=0.15$; [Table 2](#); [Fig. 2](#)). After correcting for density, leafhopper richness was positively related with elevation ($R^2=0.51$; [Table 2](#); [Fig. 3](#)) and Shannon's diversity index for leafhoppers increased with coffee density in the plot and was found to be statistically significant ($R^2=0.58$; [Table 2](#); [Fig. 4](#)). Results for the Breusch–Pagan test revealed no heteroscedasticity of residuals for both models ($P=0.53$ for richness and $P=0.22$ for Shannon's diversity index).

Local and landscape factors had differential effects on populations of individual leafhopper species. The abundance of *Agallia* sp. 1 was significantly decreased with habitat diversity in the surrounding landscape as well as the proportion of *Inga* spp. trees ($R^2=0.49$; [Table 3](#)). Sites dominated by low-shade management in the surrounding landscape and at higher elevations had more *Sibovia* sp. individuals. The effect of herbaceous height on *M. redundans*

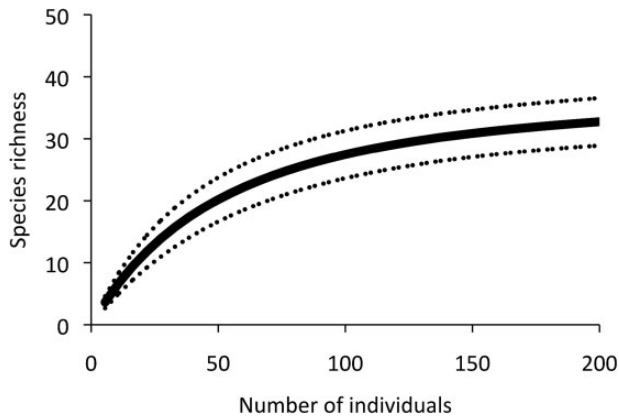


Fig. 1. Overall species accumulation curve for leafhopper species richness. Solid line represents mean of estimated richness and dotted lines represent the upper and lower bounds of the 95% confidence interval.

Table 2. Results of mixed effects models for response of abundance, richness and Shannon's diversity index to local and landscape factors

	Estimate \pm SEM	z	P
Abundance			
Low-shade coffee land-use	9.3 \pm 3.6	2.57	0.0163*
Richness			
Abundance	0.069 \pm 0.009	7.4	1.16E-13
Elevation	0.001 \pm 0.0005	2.4	0.0154*
Shannon's diversity index			
Abundance	0.08 \pm 0.013	6.3	0***
Coffee density	0.006 \pm 0.003	1.99	0.0573

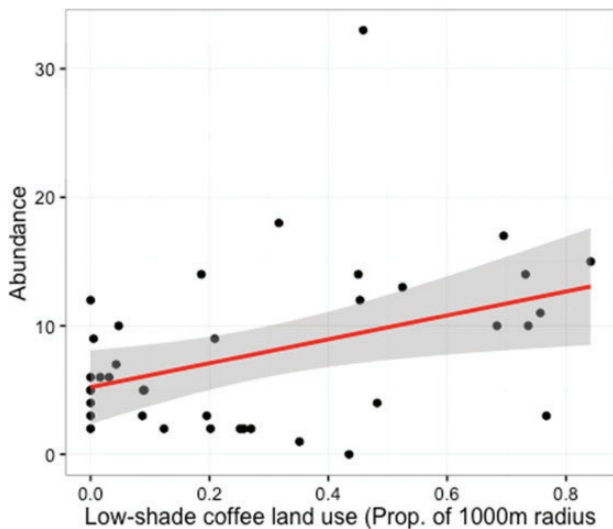


Fig. 2. Abundance of leafhoppers increased with proportion of low-shade management of coffee at the landscape level.

depended on the low-shade management of coffee in the surrounding landscape ($R^2 = 0.37$). No landscape factor was found to significantly affect abundance of *Isogonalia* sp. However, sites with a lower proportion of *Inga* spp. trees had more *Isogonalia* sp. individuals. Further, *Isogonalia* sp. abundance positively correlated with

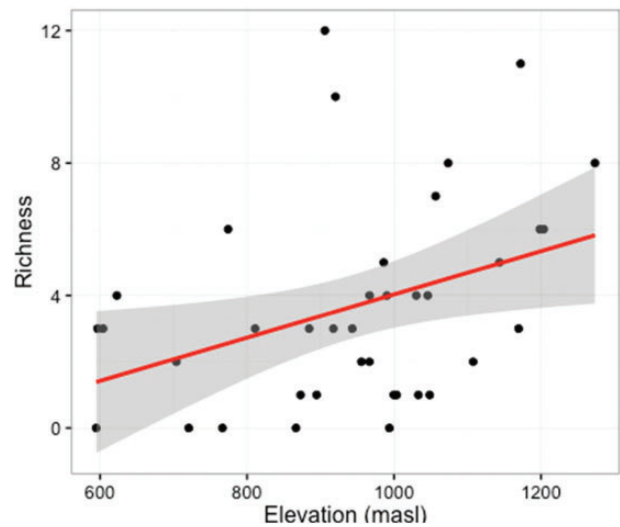


Fig. 3. Leafhopper richness increased with increase in average height of the local herbaceous layer (A) as well as estimated local shade tree richness (B) and a decrease in local tree density (C).

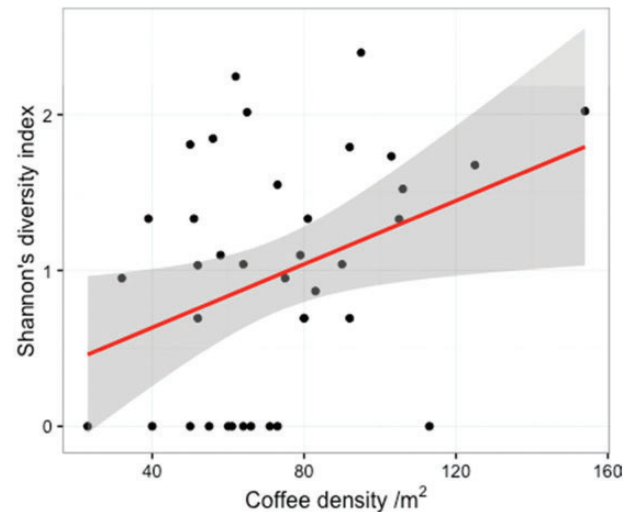


Fig. 4. Shannon's diversity index for leafhoppers increased with coffee density in the plot.

higher shade tree density ($R^2 = 0.93$). Finally, *Agallia* sp. 2 was most abundant in sites at higher elevations but decreased with diversity of habitats in the surrounding landscape. We also found that the effect of proportion of *Inga* spp. trees on *Agallia* sp. 2 was influenced by the proportion of forest in the surrounding landscape ($R^2 = 0.54$; Table 3).

Discussion

The results of this study suggest that local and landscape level coffee management factors are primarily responsible for leafhopper diversity. In particular, we found that low-shade coffee land use at large scales leads to greater leafhopper abundance, while elevation and coffee density explained leafhopper richness and Shannon's diversity, respectively.

The increase in total leafhopper abundance with increased landscape intensification (low-shade coffee land use) supports the RCH

Table 3. Results of mixed effects models for the response of individual leafhoppers to local and landscape factors

	Estimate \pm SEM	z	P
Sibovia sp.			
Elevation	0.004 \pm 0.002	2.08	0.03769 *
Low-shade coffee land-use	2.3 \pm 1.03	2.24	0.02511 *
Agallia sp. 1			
<i>Inga</i> spp. in plot	-5.66 \pm 1.47	-3.83	0.000126***
Habitat diversity (Shannon's Index)	-2.73 \pm 1.16	-2.36	0.01842*
<i>M. redundans</i>			
Herbaceous height	-0.3 \pm 0.2	-1.51	0.13133
Low-shade coffee land-use	-4. \pm 2.4	-1.81	0.07088 .
Low-shade coffee land-use \times herbaceous height	0.92 \pm 0.35	2.62	0.00883 **
Isogonalia sp.			
Tree density	0.01 \pm 0.005	2	0.044 .
<i>Inga</i> spp. in plot	-7.56 \pm 2	-3.78	0.000164 ***
Agallia sp. 2			
Habitat diversity (Shannon's Index)	-3.49 \pm 1.16	-3.01	0.00257 **
Elevation	0.01 \pm 0.002	2.66	0.00782 **
<i>Inga</i> spp. in plot	-7.93 \pm 2.58	-3.06	0.00220 **
Forest	-19.11 \pm 12.06	-1.58	0.1132
Forest \times <i>Inga</i> spp. in plot	48.75 \pm 21.27	2.29	0.02193 *

(Root 1973). The RCH suggests that total abundance of the pest community should increase when host plant density increases. In this case, high-shade management should dilute the density of coffee relative to low-shade management. At the same time, diversified agriculture at the local and landscape scales may support higher predator populations, which could limit pests from the top down in these habitats (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). Indeed, within coffee agroecosystems, bird predation of pests is known to be greater in high shade management (Perfecto et al. 2004) and in plantations surrounded by a greater proportion of forest (Karp et al. 2013). The observed increase in leafhopper abundance with landscape intensification in our study may be the result of both the concentration of resources and lower predation pressure in intensified areas. Nonetheless, syntheses of the literature have not always supported this hypothesis (Chaplin-Kramer et al. 2011, Veres et al. 2013). For example, in two reviews of the literature, neither Chaplin-Kramer et al. (2011) nor Veres et al. (2013) convincingly show that intensified landscapes increase pest abundance. Our findings are therefore important in supporting the RCH and/or the natural enemies' hypothesis at the landscape scale.

Our results reflect that leafhopper richness and Shannon's diversity find variable support for the RCH, which suggests that leafhopper diversity should increase with increased non-crop vegetative abundance or diversity. Leafhopper richness increased with elevation and Shannon's diversity increased with coffee density, contrary to the RCH. An increase in pest diversity with increased focal crop density could be expected if most herbivores found are specialists of the focal crop, where each species would increase due to a concentration of resources. For example, a review of the insect herbivore abundance in polyculture and monoculture crop fields found that 51.9% (130/220) of monophagous (specialist) herbivores increased in monocultures, while only 7.7% (17/220) increased in polycultures (Andow 1991). Further, 28.4% (19/67) of polyphagous (generalist) herbivores increased in monocultures, while 40.3% (27/67) increased in polycultures (Andow 1991). However, while we are aware that at least a few of the species we studied consume coffee, none should be considered coffee specialists (Gonthier, personal observation). Thus, this hypothesis seems unlikely. Alternatively, increased coffee productivity could facilitate leafhopper richness.

Given that low-shade coffee systems have increased fertilization and planting density, it is possible that this productivity may promote herbivore diversity. Greater productivity can lead to greater herbivore diversity through a number of mechanisms including: increased abundance of rare resources, greater persistence of rare species, or through density dependent effects (Siemann 1998). Leafhoppers, like other xylem-feeding insects, are nitrogen limited (Mattson 1980), thus increased nitrogen fertilization may improve the persistence of species that feed on coffee. Yet another alternative explanation of increased richness with intensification could be that greater predation in high-shade coffee results in fewer species (as in Perfecto et al. 2004). Hence, it is plausible that the combined effects of more readily available resources and lower predation pressure could lead to greater richness. However, we can only provide speculation and more research is needed to determine the mechanism behind this pattern.

We found that the richness of leafhoppers was greater at higher elevations. Two of the most abundant leafhoppers, *Sibovia* sp. and *Agallia* sp.2 were also found to be more abundant at higher elevations. Montane tropical communities, in particular, are affected by climatic changes as the temperature at lower elevations shifts to higher elevations. Studies of bird and moth assemblages showed that these groups have shifted up slopes to cope with climate change (Chen et al. 2009, Forero-Medina et al. 2011). If climate change continues in this study region, we might expect to see more leafhopper species at higher elevations. It is also possible that more leafhopper species were found at higher elevations because they may be released from their natural enemies. A recent study conducted across the same region as this study, reported a lower abundance and richness of spiders at higher elevations. As spiders are generalist predators this finding may represent a reduction in the potential biocontrol services found at higher elevations (Hajian-Forooshani et al. 2014). A simultaneous shift of biological control to lower elevations and herbivore diversity to higher elevations may be problematic to coffee production because although leafhoppers are only considered minor pests in coffee, they can be important plant disease vectors. Some leafhopper species carry the bacterium (*X. fastidiosa*), responsible for causing diseases in a number of important commercial plants like almonds, grapes, citrus, alfalfa, coffee, and

ornamentals (Li et al. 2001, Godoy et al. 2005). Most of the species found in the Cicadellinae subfamily have been observed to transmit *X. fastidiosa* (Redak et al. 2004). Recent reports of *X. fastidiosa* infecting coffee in Costa Rica and Brazil (Beretta et al. 1996, Rodriguez et al. 2001) implicate leafhoppers as disease vectors in those regions. Although incidence of coffee leaf scorch or crespada disease caused by *X. fastidiosa* is not reported in the Soconusco region of Mexico, it is possible that leafhoppers pose a future risk in vectoring these diseases. Our study highlights the need to understand the factors that affect the population distribution of leafhoppers in order to mitigate potential risks.

Only two other studies, to our knowledge, have investigated the distribution of leafhoppers across an intensification gradient of coffee agroecosystems. Ramos (2008) found that species richness was positively correlated with fallows in the surrounding landscape. In addition, forest cover in the landscape positively correlated with leafhopper abundance at 100 m scale, but not at the 500 m scale. Contrarily, pasture at both 100 and 500 m scales was negatively correlated with total abundance. The differences between our findings and Ramos' (2008) could be due to the difference in the regional land use composition. While our study area was dominated by coffee land use (94%), with only small forest fragments consisting of roughly 6% of the regional land area, Ramos' study area had a greater diversity of agricultural land uses (28% pasture, 14% coffee, 6% sugarcane, and 3% other crops), and a higher percentage (40%) of forest cover as compared with our study area. Besides *Agallia* sp.2, forest fragments in the surrounding landscape had no effect on any of the other most abundant leafhoppers in our study. Perhaps the larger forest fragments in Ramos' (2008) study region resulted in strong effects of forests on leafhopper abundance.

Burdine et al. (2014) found that the richness and abundance of leafhoppers increases with the number of *Inga* spp. trees at the local level. *Inga* spp. (Fabaceae) form N-fixing associations with bacteria and often have higher nitrogen content than other plant species. These plants could be important for leafhopper communities because leafhoppers are often nitrogen limited (Mattson 1980). However, our results showed that the dominance of *Inga* spp. trees locally, did not correlate with the overall leafhopper abundance, but did correlate with the abundance of *Agallia* sp. 1, *Agallia* sp. 2, and *Isogonalia* sp. While our study contained a greater number of factors related to coffee agricultural intensification and covered a much larger regional extent across many more farms, Burdine et al. (2014) studied leafhoppers during both the rainy and dry seasons, but did not investigate the effects of landscape characteristics. Perhaps there is a seasonal component to the importance of *Inga* spp. for overall leafhopper abundance. Furthermore, in our study larger-scale landscape effects of management may have influenced the strength of the effect of local shade tree composition. Interaction between local and landscape factors were also seen in the effects of herbaceous height on abundance of *M. redundans*, which depended on the proportion of low-shade coffee land use. Indeed, effects of local level management factors can change with surrounding landscape and this has been hypothesized in other systems (Tscharntke et al. 2005, Batáry et al. 2011).

We found that abundance of only two out of the five most abundant species *Sibovia* sp. and *M. redundans* was influenced by low shade coffee use in the landscape despite our results for total leafhopper abundance. In the case of *M. redundans*, the effect of the height of herbaceous cover was influenced by the proportion of low-shade coffee land use. These results are in support of the RCH. However, we also found that habitat diversity in the landscape

negatively affected the abundance of both the *Agallia* spp., suggesting a possible preference for a more homogeneous or simple landscape.

Our results indicate that coffee management at both the local and landscape level are important drivers of leafhopper diversity. Although these insects in the family Cicadellidae are not considered a major threat to coffee, some of them are vectors for diseases and pose potential risk to future coffee production. Our results are also important in explaining the factors that play a key role for the conservation of these insects in light of global land-use change.

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Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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