El Colegio de la Frontera Sur

# La diversidad y abundancia de avispas parasitoides dependen del manejo y la temporada en cultivos de café robusta (*Coffea canephora*)

Tesis
presentada como requisito parcial para optar al grado de
Maestro en Ciencias en Recursos Naturales y Desarrollo Rural
Con orientación en Entomología Tropical

Por

Sergio Salvador Zapata Martínez

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Las personas abajo firmantes, miembros del jurado examinador de:

Sergio Salvador Zapata Martinez

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hacemos constar que hemos revisado y aprobado la tesis titulada “La diversidad y abundancia de avispas parasitoides dependen del manejo y la temporada en cultivos de café robusta (*Coffea canephora*)”

para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**

| | Nombre | Firma |
|---|---|---|
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| Asesor/a | Dr. Julio Cesar Rojas León | ______________________ |
| Asesor/a | Dr. José Armando Alayón Gamboa | ______________________ |
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| Sinodal suplente | Dra. Rebeca González Gómez | ______________________ |

# Dedicatoria

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# Resumen

La sustitución de *Coffea arabica* L. por *C. canephora* Pierre ex Froehner (café robusta) ha causado la pérdida de árboles de sombra en los cafetales de la región del Soconusco en Chiapas, México. Los cafetales de sombra son una fuente de refugio para la biodiversidad. Este estudio investigó si la pérdida de vegetación afectaba a la riqueza y abundancia de las avispas parasitoides, organismos que tienen un papel relevante en la regulación de las poblaciones de insectos herbívoros. Se tomaron muestras de avispas parasitoides con trampas de sartén amarilla en 24 cafetales de robusta con tres grados diferentes de manejo agrícola (bajo, moderado, intensivo) en las estaciones seca y lluviosa. También se registraron la riqueza y la cobertura de los árboles de sombra, la cobertura herbácea, y la incidencia del minador de la hoja del café (*Leucoptera coffeella*) y de la broca del café (*Hypothenemus hampei*). En total, se registraron 230 morfoespecies de avispas parasitoides, representadas en 25 familias. Las familias más abundantes fueron Diapriidae, Encyrtidae, Ceraphronidae y Scelionidae. Las familias Scelionidae, Encyrtidae, Ichneumonidae, Braconidae y Mymaridae fueron las mejor representadas. La mayor riqueza de avispas parasitoides se encontró durante la estación de lluvias, mientras que la mayor abundancia se encontró durante la estación seca. El efecto de la intensidad del manejo agronómico de los cafetales de robusta en la riqueza y abundancia de avispas parasitoides varió de acuerdo con las familias de parasitoides. Los Encyrtidae, Mymaridae y Trichogrammatidae se asociaron a las plantaciones de manejo intensivo, mientras que los Ceraphronidae y Diapriidae se asociaron a las plantaciones sometidas a un manejo moderado. Otras familias como Braconidae, Eulophidae, Ichneumonidae, Pteromalidae y Scelionidae no se vieron afectadas por la intensidad del manejo agronómico. Concluimos que para la conservación de las avispas parasitoides en los sistemas cafeteros se deben considerar factores como la intensidad del manejo agronómico, la cobertura y diversidad de la vegetación y la época del año.

**Palabras clave:** Manejo del hábitat; Biodiversidad; Conservación de insectos; Deforestación, Chiapas

## Contenido

# I. Introducción

El café es uno de los productos básicos agrícolas más comercializados y el principal cultivo comercial en los países tropicales (Infante 2018). Además, los agroecosistemas cafetaleros son considerados fuente de refugio para la biodiversidad (Moguel y Toledo 1996). Sin embargo, las múltiples crisis del café, como la caída de los precios en el mercado internacional, la suspensión de apoyos gubernamentales y la afectación de problemas fitosanitarios y plagas, han llevado al sector cafetalero a enfrentar un panorama complejo (Escamilla-Prado 2017)

En México, los productores de café se han interesado en sustituir la sombra natural diversa por sistemas simplificados. Como consecuencia, muchos productores han reducido la cantidad de sombra del cafetal en la búsqueda de incrementar la producción, dando como resultado la pérdida de la biodiversidad (Perfecto et al. 1997; Romero-Alvarado et al. 2002). En las zonas bajas del Soconusco, Chiapas, el incremento en la superficie de café robusta (*Coffea canephora* Pierre ex Froehner), es decir, la sustitución de *C. arabica* por *C. canephora*, proceso al que se le ha llamado “robustización” (Barrera 2016), ha ocasionado una reducción de la sombra en las plantaciones cafetaleras de la región. A esta situación se suma el desconocimiento de la entomofauna y su función en los cafetales por parte de muchos agricultores, lo cual ha llevado a la aplicación extensiva e indiscriminada de plaguicidas (Righi et al. 2013) y, en consecuencia, la eliminación de la diversidad de la fauna en general, y de los insectos benéficos en particular.

La manipulación del hábitat con el fin de crear condiciones que favorezcan las poblaciones de enemigos naturales se ha vuelto una parte fundamental para el control biológico por conservación (CBC). De acuerdo a Vázquez et al. (2008) la conservación de enemigos naturales consiste en proteger, favorecer el desarrollo y manipular a estos organismos en el agroecosistema, con el propósito de incrementar la actividad reguladora de las especies más eficientes o de lograr tasas de regulación como resultado de la acción conjunta de las diferentes especies. Para ello, el manejo de las plantas juega un papel muy importante en el CBC, pues mantienen poblaciones de enemigos naturales al proporcionar presas, recursos florales para los adultos y microclimas adecuados como refugio (Powell 1986; van Emden 1990). Por lo tanto, la diversificación de la composición de las comunidades vegetales podría alentar a los enemigos naturales a suprimir las poblaciones de insectos fitófagos (Tooker y Hanks 2000).

Entre los enemigos naturales destacan las avispas parasitoides, los cuales son reguladores importantes de muchas plagas en cultivos de importancia, y son ampliamente usados en programas de control biológico. Además, responden a variaciones en la complejidad del hábitat (LaSalle y Gauld 1993), por lo que han sido un modelo interesante para los estudios de diversidad (González-Moreno et al. 2018). Con respecto a las investigaciones dirigidas a la diversidad de himenópteros para el control de plagas en café, se han registrado distintos parasitoides atacando a una variedad de insectos de importancia agrícola en el estado de Chiapas. Entre estas investigaciones se han observado himenópteros parasitando al minador de la hoja del café *Leucoptera coffeella* (Lomeli-Flores et al. 2009). Además se han realizado liberaciones de diferentes parasitoides contra la broca del café *Hypothenemus hampei* como una estrategia de control biológico clásico (Gómez Ruiz et al. 2010).

El presente estudio investigó el efecto de la intensidad del manejo sobre las plantaciones de café robusta y si el grado de intensidad influye en la pérdida de vegetación, así como de la riqueza y abundancia de las avispas parasitoides. Además, se relacionó el posible impacto del manejo, la temporada del año y las avispas parasitoides sobre alguno de los insectos considerados plagas relevantes en este agroecosistema. El estudio se realizó durante dos temporadas del año, temporada seca y de lluvias en la región baja del Soconusco, Chiapas. Se discuten los resultados a la luz de cuatro hipótesis planteadas: i) la intensidad del manejo de las parcelas experimentales tendrá un efecto significativo sobre la riqueza y cobertura de la sombra y cobertura del suelo; ii) la abundancia y diversidad de parasitoides presentan una variación significativa entre las temporadas del año e intensidad del manejo; iii) el manejo de la sombra, la cobertura del suelo y la presencia de ciertas especies de árboles afectan de manera distinta y significativa a las familias de parasitoides; y iv) la presencia de parasitoides tiene un efecto significativo sobre algunas plagas del café.

# II. Diversity and abundance of parasitoid wasps in robusta coffee crops (*Coffea canephora* Pierre ex Froehner) depend on both the degree of agricultural management and year season in the South of Chiapas, Mexico

Sometido a: Agriculture, Ecosystems & Environment

Agriculture, Ecosystems and Environment

Corresponding author:

Juan F. Barrera
El Colegio de la Frontera Sur,
Carretera Antiguo Aeropuerto km
2.5, Tapachula, Chiapas
CP 30700, Mexico.
Email: jbarrera@ecosur.mx

Original paper

# Diversity and abundance of parasitoid wasps depend on the intensity of agricultural management and the season in robusta coffee crops (*Coffea canephora*)

Sergio Zapata-Martínez[1], Juan F. Barrera[1*], José Armando Alayón-Gamboa[2], Julio C. Rojas[1]

[1] Arthropod Ecology and Pest Management Group, Department of Agriculture, Society and Environment, El Colegio de la Frontera Sur, Carretera Antiguo Aeropuerto km 2.5, 30700, Tapachula, Chiapas, Mexico. Emails: biol.sergiozm@hotmail.com, jbarrera@ecosur.mx, jrojas@ecosur.mx

[2] Preservation and Restoration of Forests Group, Department of Biodiversity Preservation, El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Ciudad Industrial, 24500 Lerma Campeche, Campeche, México. Email: jalayon@ecosur.mx

* Corresponding author

## Abstract

The replacement of *Coffea arabica* L. by *C. canephora* Pierre ex Froehner (robusta coffee) has caused to the loss of shading trees in coffee plantations from the Soconusco region in Chiapas, Mexico. Shaded coffee plantations are a source of shelter for biodiversity. In this study, we investigated if the vegetation lost affected the richness and abundance of parasitoid wasps, organisms that have a relevant role in the regulation of herbivorous insect populations. Parasitoid wasps were sampled with yellow pan traps in 24 robusta coffee plantations with three different degrees of agricultural management (low, moderate, intensive) in the dry and rainy seasons. Richness and coverage of the shading trees, herb coverage and herbivory incidence of the coffee leaf miner (*Leucoptera coffeella*) and coffee berry borer (*Hypothenemus hampei*) were also recorded. Overall, 230 morphospecies of parasitoid wasps were recorded, represented in 25 families. The most abundant families were Diapriidae, Encyrtidae, Ceraphronidae, and Scelionidae. The Scelionidae, Encyrtidae, Ichneumonidae, Braconidae and Mymaridae families were best represented. The greatest parasitoid wasp richness was found during the rainy season, whereas the greatest abundance was found during the dry season. The effect of the agronomic management intensity of robusta coffee plantations on the richness and abundance of parasitoid wasps varied in accordance with the parasitoid families. Encyrtidae, Mymaridae, and Trichogrammatidae were associated with the intensive management plantations, whereas the Ceraphronidae y Diapriidae were associated with plantations subject to a moderate management. Other families such as Braconidae, Eulophidae, Ichneumonidae, Pteromalidae and Scelionidae were not affected by the agronomic management intensity. We concluded that for parasitoid wasp conservation on coffee systems should considered factors such as

agricultural management intensity, vegetation coverage and diversity, and the season of the year.

**Key words:** Habitat management; Biodiversity; Insect conservation; Deforestation, Chiapas

## 1. **Introduction**

Coffee is one of the products of the Mexican agricultural with the most economic, sociocultural and environmental importance. Coffee activity is essential for Mexican rural development, as it integrates production chains, generates foreign exchange, provides a livelihood for many small producers and indigenous groups, and offers environmental services of vital importance. Coffee cultivation is done under a great diversity of social, economic and ecological conditions. Nevertheless, *Coffea arabica* L. is mostly cultivated by small producers by means of shading trees systems predominates with over 95% (Díaz-Cárdenas *et al.*, 2017; Escamilla-Prado and Díaz-Cárdenas, 2002; Escamilla-Prado and Landeros-Sánchez, 2016; López-Morgado *et al.*, 2013; Manson and Sosa-Fernández, 2019; Moguel and Toledo, 1996, 1999).

Coffee plantations growing under shading trees have large ecological importance, as they provide several services such as a larger amount of nutrients, and they have a greater hydrological and microclimatic balance in comparison with those grown under the full sun (Barrera, 2002; DaMatta, 2004; Lin, 2007; Muschler, 2006). Besides, shaded coffee plantations are a source of shelter for biodiversity, as these have a higher number of tree species. It is known that the functional diversity of coffee plantations is directly correlated to the conservation of many plant and animal taxa (Manson and Sosa-Fernández, 2019;

Moguel and Toledo, 1996, 1999; Perfecto *et al.*, 1996). Thus, shaded coffee plantations contribute to the conservation of plants, insects, spiders, birds, reptiles, and mammals (Donald, 2004; Hajian-Forooshani *et al.*, 2014; Jha *et al.*, 2014; Komar, 2006; López-Gómez *et al.*, 2008; Philpott *et al.*, 2008). Moreover, scientific evidence shows that the interaction networks between the different taxonomic groups can keep the system free of pest outbreaks (Liere *et al.*, 2012; Perfecto *et al.*, 2010; Perfecto and Vandermeer, 2015).

Unfortunately, many producers have reduced the amount of shade on their coffee plantations aiming a coffee production increase, resulting in the loss of biodiversity (Perfecto *et al.*, 1997). For instance, between 1970 and 1990, almost 50% of shaded coffee farms in Latin America became low-shade systems (Perfecto *et al.*, 1996). Low-shaded plantations, called “specialized system” by Escamilla-Prado *et al.* (2002), are characterized by the high-density cultivation of highly productive coffee trees (> 3000 trees/ha) with varieties that are tolerant of direct sunlight, low-sized (2-3 m) and a dense foliage (Borkhataria *et al.*, 2012).

The reduction or elimination of shading trees in coffee plantations affects the habitat diversity and, consequently, the fauna diversity. In addition, the lack of knowledge of the entomofauna and its role in coffee plantations has led to an extensive and indiscriminate use of pesticides by many farmers (Righi *et al.*, 2013). Thus, the reduction of shade and the indiscriminate use of pesticides could harm ecological processes, altering host and food searching, and survival of natural enemies (Chisholm *et al.*, 2014; Crowder and Jabbour, 2014; Fiedler *et al.*, 2008; Fonseca *et al.*, 2017; Frank, 2010; Jonsson *et al.*, 2008).

Parasitoid wasps stand out among the natural enemies as important regulators of many herbivore insect species. Parasitoids respond to variations of habitat complexity (LaSalle and Gauld, 1993). Consequently, they are an interesting model for diversity studies (González-Moreno *et al.*, 2018). Thereon, it has been found that these insects' life cycles are highly sensitive to drastic reductions of their populations, even leading to the local extinction of some species (González-Moreno *et al.*, 2018; Hochberg and Ives, 2000). In this way, and from a practical point of view, the manipulation of the habitat and the use of ecologically and physiologically selective pesticides are conservation biological control actions aimed at developing conditions in the agroecosystem that protect and promote parasitoid populations (Landis *et al.*, 2000; Mills *et al.*, 2016; Wyckhuys *et al.*, 2013).

As of the increase of the robusta coffee's area (*Coffea canephora* Pierre ex Froehner) due to the low productivity of *C. arabica* in lower areas and to its susceptibility to the attack of the coffee leaf rust, *Hemileia vastatrix* Berk. *et* Br. a significant increase of deforestation has been observed in the Soconusco coffee region in the South of Chiapas, Mexico (Barrera, 2016; Barrera and Gómez-Ruiz, 2019). The replacement of *C. arabica* by *C. canephora*, meaning, the change of soil usage in coffee growing regions called 'robustization' (Barrera, 2016), has been encouraged by public and private policies that favor the planting, cultivation, and marketing of coffee made from four improved clones of *C. canephora*. This coffee technology based on improved clones of *C. canephora* (Méndez-López *et al.*, 2017), has led to a reduction of shade in the region's coffee plantations.

On the assumption that the reduction or elimination of shading trees in robusta coffee plantations may affect parasitoid species that play an important role in the natural regulation of herbivore insects in coffee plantations, this study set the objective of determining the effect of the intensity of *C. canephora* plantations management on the diversity and abundance of parasitoid wasps during the dry and rainy seasons in the South of Chiapas. The specific objectives of this study were: i) determine the effect of management intensity of experimental plots on tree richness, and shade and ground coverage; ii) identify the variations of abundance and diversity of parasitoid wasps between the seasons of the year and the management intensity; iii) determine the effect of shade management, ground coverage, and the presence of certain tree species on parasitoid families; and iv) establish the relation between the presence of parasitoids with some herbivore insect species associated with coffee plants.

## 1. **Methodology**

### *1.1.Study area and sampling periods*

The study area was located in the Soconusco region to the South of Chiapas, Mexico. Specifically, the sampling was done in plantations cultivated with the improved clones of *C. canephora* established in the municipalities of Cacahoatan, and Tapachula. The samplings were performed in 24 plantations, trying to ensure that these were cultivated in a range of tree coverage from abundant to no shading. The plantations' elevation varied from 450 to 750 masl. The selected plantations were sampled once in each of the two seasons of the year (dry and rainy) in order to accumulate a total of 48 samplings. The first 24 samplings were done from February to April (dry season), and the remaining from July to August (rainy season) in 2019. The precipitation data was obtained from the coffee farm Alianza (15° 2'39.39" N; 92°10'5.66" O, 684 masl). The accumulated precipitation recorded during the sampling period was 71.7 mm for the dry season, and 626.2 mm for the rainy season (**Fig. S1**).

### *1.2.Experimental plots and recorded variables*

An experimental plot of 20 $m^2$ was established inside of 24 coffee plantations. In each plot the following variables were recorded: a) plantation's management intensity, b) richness and shading tree coverage, c) ground coverage, d) diversity and abundance of parasitoid wasps, and e) abundance of some herbivore species relevant to coffee cultivation.

Plantation's management intensity. This variable was determined through semi-structured interviews done to the plantations' owners and taking into account the information from the field samplings; including questions about the agricultural activities in plantations in regards to the management of weeds, diseases and insect pests, soil conservation, as well as the type and frequency of agrochemicals application throughout the year. The age (years) of the plantation, the geographical location, and the altitude (masl) of the experimental plots were also recorded.

Coverage and shading tree richness. The shade coverage (ShC), defined as the percentage of foliage coverage that darkens the open sky as seen from the ground (Feldpausch *et al*., 2005), was determined by means of the "grid method" (ANACAFE, 2006). The method consists of recording the presence/absence of shading tree foliage above each one of the coffee plants that were in the experimental plots. Considering that the diversity of shading trees in coffee plantations in Mexico may vary considerably throughout a cultivation intensity gradient (Moguel and Toledo, 1999), the shading tree richness (STR) (number of species) was also recorded. The experimental plots' shading tree species were identified with producers' help and by consulting the Chiapas vegetation book (Miranda, 1998). Furthermore, each experimental plot was categorized according to the presence or absence of fruit trees. A "plot with fruit trees" was that with at least one fruit tree species.

Ground coverage. This variable consisted of determining the relative presence of the following three categories of ground coverage in each experimental plot: herb coverage (HC), leaf litter (LL), and bare ground (BG). We used the "shoe tip" method (Guharay *et al.*, 2000), which consists of recording the presence/absence of the aforementioned coverage categories in 30 sampling points on the ground surface. Each sampling point was located between the paths formed by the coffee plant rows, at 3.0 m within rows.

Diversity and abundance of parasitoid wasps. The sampling of the parasitoids was carried out by means of five pan traps distributed in a "five of coins" design in each experimental plot. The traps consisted of 1000-ml yellow plastic containers (10 cm height and 16 cm diameter). Each trap was filled with a soapy solution (300 ml of water and 5.0 ml of soap) and placed on the ground for a 24-hour period, starting from 9:00 a.m. The parasitoids collected were preserved in vials with a 70% alcohol solution. Specimens were separated by family and morphospecies using taxonomic keys (Fernández et al., 2006; Goulet and Huber, 1993).

Abundance of coffee herbivore insect species. The incidence of herbivore insects was recorded using the "integral sampling of pests" (Guharay *et al.*, 2000), which fitted the conditions of this study. A total of 20 coffee plants per experimental plot were chosen, and a plagiotropic branch one meter from the ground was taken from each one in order to record the following variables: total number of leaves, number of leaves showing signs of insect herbivory, number of leaves showing damage of coffee leafminer, *Leucoptera coffeella* (Guérin-Méneville) (Lepidoptera: Lyonetiidae), total number of berries and bored berries by the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae). Thus, the incidence (percentage) of damaged leaves by the coffee leaf miner, leaves showing signs of insect herbivory, and berries bored by the coffee berry borer were determined.

### *1.3.Data analysis*

All analyses were made with the R statistical software (v.6.3.1) (R Core Team, 2018). The effect of agronomic intensity management on the recorded variables was analyzed by Kruskal-Wallis post-hoc tests performed through the "Agricolae" package (de Mendiburu, 2019).

The effect of the season and plantation management on diversity and abundance of parasitoid wasps was determined in two ways: considering the pooled parasitoids (a mixture of all families), and grouping parasitoids by families. For the pooled parasitoids, the effective morphospecies numbers (Hill numbers) were used, and the richness or diversity of morphospecies ($q$=0), diversity based on the exponential of Shannon's entropy ($q$=1), and Simpson's rate ($q$=2) were estimated (Chao *et al.*, 2014). To demonstrate the diversity, total morphospecies accumulation graphs were made per season of the year and plantation management intensity through rarefaction and extrapolation curves (R/E). These curves were made based on the size of the sample with 95% confidence intervals by using a bootstrap method with 200 replications through the iNEXT package (Hsieh *et al.*, 2016). Therefore, the maximum size was established by extrapolating at double the size of the reference sample (Hsieh *et al*., 2016). Both the pooled parasitoid abundance and richness by family were represented with average (± standard error) graphs between the seasons and management intensity, and Kruskal-Wallis post-hoc comparisons.

The effect of the shade and ground coverage on parasitoid abundance by families in the experimental plots were examined by using Non-metric multidimensional scaling (nMDS). We use the Gower (1971) distance matrix for mixed variables (categorical and numerical) by means of the "daisy" function of the cluster package (Mächler *et al.*, 2012). This matrix was used to create the ordination of the nMDS through the "metaMDS" function of the vegan package (McCune and Grace, 2002; Oksanen et al., 2019). Subsequently, a graph (*triplot*) was made with the group of recorded variables and the parasitoid families by adjusting them to the nMDS ordination distance matrix with the "envfit" function of the vegan package.

The comparison of damaged leaves by the coffee leaf miner, leaves with insect herbivory, and damaged berries by the coffee berry borer between the dry and rainy seasons and the experimental plot types of management was done by means of a Kruskal-Wallis non-parametric test. Furthermore, generalized lineal models (GLM) were created with a Poisson distribution for abundance, parasitoid richness, Shannon's diversity rate, season, and management intensity and other variables recorded in field. Lastly, analyses of variance of the GLM models were made to determine the influence of these variables on the herbivore insects.

## 2. **Results**

### *2.1.Management intensity of experimental plots*

In total, four plots were classified as low-intensity management plots; 12 as moderate, and eight as intense (**Table 1**). In general, more agrochemicals were applied in intense-management plots. The age of plantations varied from 5 to 13 years. The average age (±

standard error) of the low-intensity coffee plants (10.7 ± 1.0 years old) was similar to the moderate management plots' age (9.1 ± 0.3 years old) but different than the age of intense management plots (7.7 ± 0.5 years old) ($x^2 = 7.12$, df = 2, $P = 0.028$). Experimental plots with low and moderate agronomic management were located around the 500 masl, in contrast to intense management plots that were located on average altitude of 714 masl ($x^2 = 31.41$, df = 2, $P < 0.001$) (**Table 1**).

The shade coverage (ShC) in experimental plots varied from 0 to 96%: as increased the intensity in the management, decreases the shade coverage ($x^2 = 30.09$, df = 2, $P < 0.001$). Coverage was found to be 75.3% (± 4.9) in low-intensity management, 50.9% (± 3.4) in moderate management, and 15.4% (± 4.2) in intense management (**Table 1**).

Ground coverage type also changed depending on the management intensity ($x^2 = 9.92$, df = 2, $P = 0.006$). The presence of herb coverage (HC) was greater in plots with intense management (49.1% ± 6.0) respect to plots with moderate management (27% ± 2.9), and was similar with low-intensity management (37.5% ± 5.2). The presence of leaf litter (LL) was affected by management ($x^2 = 16.94$, df = 2, $P < 0.001$). There was a greater leaf litter coverage in plots with low (53.7% ± 6.2) and moderate (64.7% ± 2.8) intensity management than in those with intense management (34.5% ± 4.8). The presence of bare ground (BG) was also influenced by management ($x^2 = 5.85$, df = 2, $P = 0.05$). The presence of bare ground was greater in plots with intense management (15.8% ± 2.9) in comparison to moderate management (8.1% ± 1.6), and was similar to that seen in low-intensity management (8.7% ± 2.9) (**Table 1**).

The shading trees richness (STR) decreased significantly as plots went from a low-intensity management (4.25 ± 0.4 trees), to a moderate management (2.83 ± 0.2 trees), up to an intense management (0.62 ± 0.1 trees) ($x^2 = 30.09$, df = 2, $P < 0.001$) (**Table 1**). In total, 17 species of shading trees were recorded, out of which seven (41.2%) were fruit trees. The more common shading trees were *Inga* spp., *Theobroma cacao*, *Aspidosperma megalocarpon,* and *Musa* sp. (**Table S1**).

### *2.2.Diversity and abundance of parasitoid wasps*

Overall, 2,365 parasitoid wasps were collected, which represented 230 morphospecies from 25 families. The most abundant families were Diapriidae (587 individuals, 24.8%), Encyrtidae (437 individuals, 18.5%), Ceraphronidae (350 individuals, 14.8%), and Scelionidae (289 individuals, 12.2%). The other parasitoid families had an amount fewer than 150 individuals, and in some cases, only one individual was collected (*e.g.*, Agaonidae, Chalcididae, Embolemidae and Torymidae). As for richness, the Scelionidae family was best represented with 28 morphospecies, followed by Encyrtidae, and Ichneumonidae with 22 morphospecies from each, and Braconidae and Mymaridae with 20 morphospecies each (**Table 2**).

On the contrary, the diversity rates for the pooled set of parasitoid wasps was found to be 230 (q=0) morphospecies observed, per Hill’s numbers calculation; whereas the Shannon rate (q=1) determined 57.5 morphospecies, and Simpson’s (q=2) was 24.1 morphospecies, where estimated coverage was 96.4% (**Fig. 1a**).

### *2.3.Effect of the season and management of diversity and abundance of parasitoid wasps*

There were no differences between seasons of the year with regard to the richness of species (q=0); notwithstanding, Shannon (q=1), and Simpson's (q=2) rates revealed that there was a greater diversity of parasitoids during the rainy season (**Fig. 1b**). Moreover, parasitoid wasp abundance differed between the two seasons ($x^2 = 8.6995$, df = 1, $P = 0.003$). A greater number of parasitoid wasps (1, 521) were recorded during the dry season (February to April) compared to that from the rainy season (July to August), where 844 individuals were collected (**Fig. 2a**). On the other hand, the management intensity in experimental plots did not influence significantly on the total abundance and richness of the parasitoid wasps (**Fig. 1c y 2b**).

### *2.4.Effect of the season and management of diversity and abundance on parasitoid wasp families.*

There was a change in the abundance of some parasitoid wasp families depending on the season of the year (**Fig. 3a**). Diapriidae, Ceraphronidae, Eulophidae and Trichogrammatidae were more abundant during the dry season than during the rainy season ($P<0.05$). In contrast, Ichneumonidae was more abundant on the latter season ($P<0.05$). The abundance of other families such as Braconidae, Encyrtidae, Mymaridae or Scelionidae was not affected by the season of the year ($P>0.05$).

41.7% out of 12 of the most abundant parasitoid wasp families were affected by plot management intensity. The affected families displayed a different response (**Fig. 3b**). Encyrtidae and Trichogrammatidae were more abundant as plot management intensified ($P<0.05$). In other cases, such as Diapriidae, Mymaridae, and Platygastridae, even though the abundance was greater in intense-management plots than in those with moderate management ($P<0.05$), there were no differences between the intense-management and low-management plots (*P*>0.05). Some of the more abundant families that were not affected by the management were Braconidae, Ceraphronidae, Eulophidae, Pteromalidae, and Scelionidae (*P*>0.05). The rest of the families turned out to be underrepresented in the sampling (**Table 2**).

As for morphospecies richness, the families Eulophidae, Figitidae, Ichneumonidae, Pteromalidae, and Trichogrammatidae changed significantly depending on the season of the year. Eulophidae, Pteromalidae, and Trichogrammatidae presented a greater richness during the dry season, and Figitidae, and Ichneumonidae during the rainy season (**Fig. 4a**).

The management intensity only affected five out of the 12 families (*P*<0.05) regarded as the richest: Diapriidae, Encyrtidae, Mymaridae, Pteromalidae, and Trichogrammatidae. In this regard, the richness of Encyrtidae was observed to go up as plot management increased. An opposite response was seen in the families Pteromalidae and Trichogrammatidae. More complex effects of management intensity were found on the richness of Diapriidae and Mymaridae. With Diapriidae, there was a trend towards a greater morphospecies richness in moderate-management plots, whereas Mymaridae was richer in intense-management plots. Nevertheless, there were no significant differences found in both families on low intensity management (**Fig. 4b**).

### *2.5.Effect of the shade and ground coverage on parasitoid abundance (nMDS)*

The result of the analysis of parasitoid abundance with the nMDS ordination, grouping experimental plots per management intensity, shading tree coverage, shading tree richness and the presence or absence of fruit trees is presented in **Fig. 5**. Intense-management plots were grouped towards the left of the figure, being set apart from the moderate and low-management plots (**Fig. 5a**). The plots under intense management presented the less percentage of coverage (**Fig. 5b**) and richness of shading trees (**Fig. 5c**). As for moderate and low-management plots, a greater heterogeneity was found for both variables, furthermore, only these two types of management included fruit trees among their shading trees (**Fig. 5d**).

Conversely, a relation between the parasitoid families according to the intensity of management was found (**Fig. 6** and **Table 2S**). The Encyrtidae, Mymaridae, and Trichogrammatidae families were associated with the intense-management plots, whereas Ceraphronidae and Diapriidae were associated with plots subject to a moderate management. On the other hand, the Ichneumonidae family was significantly correlated to ordination; however, it did not show a clear relation with any of the plot management intensities.

Age of the plantation (Age), altitude (Alt), herb coverage (HC), and bare ground (BG) correlated to intense-management plots; particularly, the correlation between these plots and altitude was especially strong. The shading tree richness (STR), the shade coverage (ShC), and the leaf litter (LL) were correlated to plots with low to moderate management (**Fig. 6, Table 3S**).

### *2.6.Relation of the recorded variables and parasitoid wasps on herbivore insects associated with coffee*

The incidence of the coffee leaf miner (*L. coffeella*), insect herbivory damage, and coffee berry borer (*H. hampei*) were influenced by the season of the year and the coffee plot management conditions (**Fig. 7**). Leaf damage caused by *L. coffella* turned out to be significantly greater (*P*<0.05) during the rainy season than during the dry season (**Fig. 7a**). Likewise, the infestation of this insect was greater (*P*<0.05) in plots with an intensive management in comparison to moderate-management plots, although no significant differences were found (*P*>0.05) respect to low management. Parasitoids (abundance, richness, and Shannon's diversity), plantation's age, and plot altitude were also associated with the incidence of *L. coffella* (**Table 4S**).

The percentage of leaves damaged by chewing insects was significantly greater during the rainy season (*P*<0.05). Leaves damage also significantly decreased as experimental plot management intensified (*P*<0.05) (**Fig. 7b**). Incidentally, the presence of parasitoids was related to leaf defoliation; however, other variables such as the season of the year, management intensity, and experimental plot altitude were related to herbivory (**Table 4S**).

Conversely, the percentage of berries damaged by the coffee berry borer was affected by both the season of the year, and the experimental plot management (*P*<0.05) (**Fig. 7c**). Coffee berry borer infestation was greater during the dry season than in the rainy season (*P*<0.05). The percentage of damaged berries increased in intense-management plots in comparison to those with low and moderate management (*P*<0.05). On the other hand, the abundance, richness and Shannon's parasitoid diversity rate were related to the incidence of this insect (**Table 4S**).

## 3. Discussion

### *3.1. Effect of management intensity on plots*

The results of this study indicated that the coverage and shading richness in *C. canephora* plantations in the Soconusco region, Chiapas, diminished as management intensified. This result is in line with the situation that arises in the field. In *C. canephora* or *C. arabica* plantations with a more intensive management, growers tend to remove the shading trees or to use “low shade” trees to increase the yields per hectare (Perfecto *et al.*, 1997, 1996; Romero-Alvarado *et al.*, 2002).

As expected, a greater leaf litter was found in low and moderate-management plots, because these plots had more coverage and shading richness. The greater accumulation of leaf litter in shaded coffee plantations in comparison to those exposed to the sun has been well documented (Staver *et al.*, 2020). It is also known that as the tree vegetation complexity increase the weed density decrease (Beer *et al.*, 1998), which may explain why there were no differences between low and intensive management with regard to herb coverage and bare ground. These results show complex interactions seen between the management of coffee plants, shading trees, and other vegetation strata such as herbs, which should be taken into account due to their possible effects on fauna.

Shaded coffee plantations are increasingly appreciated for their contribution to biodiversity conservation and ecosystem service supply (De Beenhouwer *et al.*, 2013; Tscharntke *et al.*, 2011). Furthermore, Peeters *et al.* (2003) state that more diverse shading vegetation will increase the production of other commodities in coffee plantations, such as fruit, lumber, and firewood, which diversify the diet and contribute to stabilizing the income of small coffee producers (Escalante, 1995; Herzog, 1994).

This study suggests that robusta coffee plantations with a low and moderate-management were rich in tree species, nonetheless, modernization through intense management is altering plant diversity in this agroforestry ecosystem and reducing the fruit tree species on the coffee farm.

### *3.2.Abundance and pooled diversity of parasitoid wasps*

Relatively few studies have focused on researching richness and abundance of parasitoid wasps in coffee plantations. To our knowledge, our study is the first that investigates the diversity and abundance of parasitoid wasps in plantations of *C. canephora* in the Soconusco region. In this study, a total of 2,365 parasitoid wasps with 230 morphospecies belonging to 25 families were recorded. Pak *et al.* (2015) performed a study in this same region with a sampling method similar to ours but in plantations of *C. arabica*. They recorded 164 morphospecies of parasitoid wasps in 27 families from a total of 422 collected individuals. Although both studies recorded a similar number of parasitoid wasp families, there was a marked difference in the number of morphospecies between them. Our study probably recorded more morphospecies because the samplings were done during the dry and rainy seasons, whereas the other study only collected once at the beginning of the rainy season (Pak *et al.*, 2015).

Our findings showed that Diapriidae, Encyrtidae, Ceraphronidae, and Scelionidae were the families with a greater abundance of parasitoid wasp individuals in the robusta coffee plantations. Pak *et al.* (2015) reported that Encyrtidae, Diapriidae, Ichneumonidae, and Eucoilidae were the families with the most abundance in *C. arabica* plantations. In our study, the families Scelionidae and Ceraphronidae also stand out for their abundance. As can be seen, plantations of *C. canephora* and *C. arabica* share similarities regarding the most abundant families of parasitoid wasps.

With regard to the richness, Scelionidae, Encyrtidae, Ichneumonidae, Braconidae, and Mymaridae were best represented in the robusta coffee plantations. Pak *et al.* (2015) found that families Encyrtidae, Ichneumonidae, and Braconidae were among the richest in arabica coffee plantations. Regardless of the methodological differences between both studies, this comparison suggests that robusta coffee plantations can house a parasitoid species richness similar to that found in arabica coffee plantations.

Studies on parasitoid wasp diversity in agroforestry systems such as that of the cacao (*Theobroma cacao* L.) have found relatively high abundances of families such as Braconidae, Ichneumonidae, Scelionidae, Encyrtidae, Platygastridae, and Diapriidae (Mazón, 2016; Sperber *et al.*, 2004). In our study, similarities were found as far as the relative abundance of these same families, despite the sampling method was different in the aforementioned studies (Malaise traps), which suggests that both agroforestry systems possess a similar parasitoid composition.

We did not find a significant difference between the three levels of management intensities on the total (pooled families) of parasitoid wasp abundance and richness. Even though the intensification of land use is recognized as an important driver of biodiversity decline (Herbst *et al.*, 2017; Lassau and Hochuli, 2005; Liere *et al.*, 2017; López-Gómez *et al.*, 2008), significant declines are not always observed with coffee plantation management intensification (Philpott *et al.*, 2008; Ricketts *et al.*, 2001). Nevertheless, as will be pointed out below, this effect can be clearer in the case of parasitoid wasps if the analysis is done at a family level.

As for the effect of the season of the year, Shannon and Simpson's rate showed a greater diversity of parasitoid wasps during the rainy season than in the dry season. Moreover, the parasitoid wasp abundance was significantly greater during the dry season. These results agree previous findings that indicate that insects in tropical zones, such as the Soconusco region, show a pronounced seasonality (Wolda, 1992, 1988). Regarding the richness of morphospecies, our study is in agreement with that of Young (1982); this author points out that in tropical regions with a strong seasonality, the number of active insect species rises at the beginning and declines near the end of the rainy season. In cacao agroforestry systems, the number of parasitoid families increased in both spring and summer, but decreased in winter (Sperber *et al.*, 2004). In our study, unlike parasitoid richness, which was greater during the rainy season, the abundance of parasitoid wasps was found to be greater during the dry season.

Considering that insect capture by means of pan traps can be negatively affected by rain (Chay-Hernández *et al.*, 2006), the possible underestimation of parasitoid abundance during this season is not ruled out. Furthermore, as in all insect sampling with traps, the record may be biased with regard to the real structure of the community because the trap effectiveness depends on the individual taxon and its behavior (Shapiro and Pickering, 2000).

### ***3.3.Effect of the Season and management intensity on parasitoid wasp families***

We found that the shading management, ground coverage and the presence of trees affected some of the parasitoid families. Although the factors related to agricultural management practices can affect the abundance of natural enemies (Harterreiten-Souza *et al.*, 2014), the results of our study agree with previous studies that point out that the effect of agricultural management changes on abundance and richness of various organisms depends on the taxonomic or functional groups (Hajian-Forooshani *et al.*, 2014; Liere *et al.*, 2017; Mas and Dietsch, 2016; Ricketts *et al.*, 2001; Tylianakis *et al.*, 2005). Few studies on parasitoid wasps focus on these changes, however, it seems that the vegetation characteristics may affect the abundance and diversity of some taxa (Fraser *et al.*, 2007; Rodríguez *et al.*, 2010).

The results of our study showed that, among the families with the most richness, Encyrtidae, Mymaridae, and Trichogrammatidae were associated to plots with intense management. In contrast, even though Ichneumonidae was correlated to the nMDS ordination, it did not show a defined pattern towards any kind of management. This results coincides with that of Klein *et al.* (2002), who reported that the abundance of Ichneumonidae was not affected by the land use within or outside of a forest in Indonesia. Other families found in our study such as Braconidae, Eulophidae, Pteromalidae, and Scelionidae, although abundant, were apparently not affected by the agronomic management.

It is likely that our findings were affected by other factors that were out of our control and that may have had influence on the abundance and richness of parasitoid families; these could have influenced the refuge and breeding sites, feeding habits, and host species. For instance, it has been reported that some parasitoid wasp groups prefer open, dry, and sunny habitats (Chay-Hernández *et al.*, 2006). In other cases, the habitat disruption can increase the presence of flowering plants which allure phytophagous, pollinator, predator, and parasitoid insects (Lewis and Whitfield, 1999). Rodríguez *et al.* (2010) found that abundance and number of species of Encyrtidae varied with time and it was greater during the dry season. In contrast, our data do not show evidence that this family was affected by the season of the year in the robusta coffee plantations.

### *Effect of management, season and parasitoids on herbivore species associated with coffee*

Our study showed that the damage caused by the coffee leaf miner and chewing insects was greater during the rainy season than during the dry season, whereas the opposite occurred with coffee berry borer infestation. A previous study performed in the same coffee producing region where we carried out our study indicated that the coffee leaf miner infestation was greater during the rainy season (Lomeli-Flores *et al.* 2009, 2010). These results differ with those reported by other authors found that rain acts as a mortality factor on this insect in the Neotropical region (Bacca *et al.*, 2012; Nestel *et al.*, 1994; Pereira *et al.*, 2007; Villacorta, 1980).

It is possible that the greatest infestation of coffee berry borer seen in robusta during the dry season can be explained by two events. First, the prolonged period of fructification of the robusta coffee–period that extends up to four months after November, when the rainy season is over–, and second, the migration of coffee berry borer females that begins in late December –when the arabica coffee plantation harvest has finished–, and lasts until the end of April (Baker *et al.*, 1989).

Both the coffee leaf miner and the coffee berry borer infestations were greater in intense-management experimental plots. Only herbivory caused by chewing insects decreased as experimental plot management intensified. This contrasts with the study that reported that the damage caused by caterpillars in coffee plant leaves was lesser in plantations with a low agronomic management (Sosa-Aranda *et al.*, 2018).

With regard to the coffee leaf miner, our results coincide with the reports that point out that the infestation outbreaks are associated with plantations located in low areas with intense management, particularly in plantations that have removed completely or reduced drastically the shading trees, and use insecticides for coffee leaf miner control (Barrera, 2018, 2002; Guharay *et al.*, 2001; Monterrey *et al.*, 2001). A study investigating the effect of environmental variables on the coffee leaf miner reported that the presence of this insect decreased linearly with the increase of relative humidity and the canopy coverage, whereas it increased with the temperature (Teodoro *et al.*, 2008).

Arabica coffee shading systems have been frequently reported to favor coffee berry borer infestations (Barrera, 1994; Bosselmann *et al.*, 2009; Mariño *et al.*, 2016; Teodoro *et al.*, 2008). Nevertheless, our results in robusta coffee plantations contradict this assertion, as a fewer percentage of berries bored by this pest were recorded in low and moderate-management plots, which were characterized by having a greater shade coverage.

Our study showed that the presence of parasitoid wasps was related to some of the herbivore insect species associated with coffee. In the case of herbivory by chewing insects in coffee plants, a significant correlation with parasitoid abundance and richness was not found. This result might be explained by the fact that the analysis that we carried out considered the possible herbivore taxonomic groups involved in the defoliation of coffee plants as a single or pooled group.

It was found that abundance, richness and the Shannon's diversity rate of parasitoids were significantly associated with the coffee leaf miner and the coffee berry borer. Although it is possible for the relation between parasitoid abundance and richness and these pests to be spurious, the existence of complex interactions such as those found by several authors in shaded arabica coffee plantations in the Soconusco region (Perfecto *et al.*, 2010; Perfecto and Vandermeer, 2015) cannot be ruled out. Such complex interactions are possible because at least 22 species of coffee leaf miner parasitoid wasps have been identified in these coffee plantations, which could contribute to over 40% of the total larvae mortality (Lomeli-Flores *et al.*, 2009), and parasitoid wasps have been released for the biological control of the coffee berry borer (Gómez Ruiz *et al.*, 2010).

## 4. Conclusions

This study showed that the season of the year and the robusta coffee plantation management intensity affected the richness and abundance of parasitoid wasps. Our findings point out that, the presence of some taxonomic groups of parasitoid wasps can be promoted or reduced, depending on the plantation agricultural management practices. These practices affect some herbivore insects associated with the coffee plants. Therefore, parasitoid wasp conservation for the purpose of biological control shall take into account multiple factors such as agricultural management intensity, vegetation coverage and diversity, the season of the year and the taxonomic groups of parasitoids involved. When management intensity increased in robusta coffee plantations, higher incidence of pests such as the coffee leaf miner and the coffee berry borer was promoted.

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## References

Asociación Nacional del café, (ANACAFE), 2006. Metodología para la evaliación de servicios ambientales.

Bacca, T., Saraiva, R.M., Lima, E.R., 2012. Captura de leucoptera coffeella (lepidoptera: Lyonetiidae) en trampas con feromona sexual y su intensidad de daño. Rev. Colomb. Entomol. 38, 42–49.

Baker, P.S., Barrera, J.F., Valenzuela, J.F., 1989. The distribution of the coffee berry borer (Hypothenemus hampei) in Southern Mexico: A survey for a biocontrol project. Trop. Pest Manag. 35, 163–168. https://doi.org/10.1080/09670878909371349

Barrera, J.F., 2018. Insect pests of coffee and their management in nature-friendly production systems, in: Vacante, V., Kreiter, S. (Eds.), Handbook of Pest Management in Organic Farming. CAB International, Oxfordshire, UK, pp. 477–501.

Barrera, J.F., 2016. Café robusta, ¿héroe o villano? Ecofronteras 20, 15–17.

Barrera, J.F., 2002. Principios agroecológicos para el manejo de plagas en cafetales, in: Pohlan, J. (Ed.), México y La Cafeticultura Chiapaneca: Reflexiones y Alternativas Para Los Caficultores. Shaker Verlag, Germany, pp. 201–208.

Barrera, J.F., 1994. Dynamique des populations du scolyte des fruits du caféier, Hypothenemus hampei (Coleoptera: Scolytidae), et lutte biologique avec le parasitoïde Cephalonomia stephanoderis (Hymenoptera: Bethylidae), au Chiapas, Mexique.

Doctorat de l’Université Paul Sabatier Toulouse, France.

Barrera, J.F., Gómez-Ruiz, J., 2019. Plagas y enfermedades del café: Características, manejo y retos, in: Bello-Baltazar, E., Soto-Pinto, L., Huerta-Palacios, G., Gómez-Ruiz, J. (Eds.), Caminar El Cafetal: Perspectivas Socioambientales Del Café y Su Gente. El Colegio de la Frontera Sur y Juan Pablos Editor, S.A., México, pp. 115–139.

Beer, J., Muschler, D.K., Somarriba, A., 1998. Shade management in coffee and cacao plantations. Agrofor. Syst. 38, 139–164. https://doi.org/10.7567/JJAPS.24S2.742

Borkhataria, R.R., Collazo, J.A., Groom, M.J., 2012. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agric. Ecosyst. Environ. 151, 1–5. https://doi.org/10.1016/j.agee.2012.01.025

Bosselmann, A.S., Dons, K., Oberthur, T., Olsen, C.S., Ræbild, A., Usma, H., 2009. The influence of shade trees on coffee quality in small holder coffee agroforestry systems in Southern Colombia. Agric. Ecosyst. Environ. 129, 253–260. https://doi.org/10.1016/j.agee.2008.09.004

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1

Chay-Hernández, D.A., Delfín-González, H., Parra-Tabla, V., 2006. Ichneumonoidea (Hymenoptera) Community Diversity in an Agricultural Environment in the State of Yucatan, Mexico. Environ. Entomol. 35, 1286–1297. https://doi.org/10.1603/0046-

225x(2006)35[1286:ihcdia]2.0.co;2

Chisholm, P.J., Gardiner, M.M., Moon, E.G., Crowder, D.W., 2014. Tools and techniques for investigating impacts of habitat complexity on biological control. Biol. Control 75, 48–57. https://doi.org/10.1016/j.biocontrol.2014.02.003

Crowder, D.W., Jabbour, R., 2014. Relationships between biodiversity and biological control in agroecosystems: Current status and future challenges. Biol. Control 75, 8–17. https://doi.org/10.1016/j.biocontrol.2013.10.010

DaMatta, F.M., 2004. Ecophysiological constraints on the production of shaded and unshaded coffee: A review. F. Crop. Res. 86, 99–114. https://doi.org/10.1016/j.fcr.2003.09.001

De Beenhouwer, M., Aerts, R., Honnay, O., 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agric. Ecosyst. Environ. 175, 1–7. https://doi.org/10.1016/j.agee.2013.05.003

de Mendiburu, F., 2019. agricolae: Statistical Procedures for Agricultural Research.

Díaz-Cárdenas, S., Escamilla-Prado, E., Roblero-Martínez, J.D., 2017. La cafeticultura mexicana: Cadena productiva, innovación y política pública reciente. Claridades Agropecu. 3–8.

Donald, P.F., 2004. Biodiversity Impacts of Some Agricultural Commodity Production Systems. Conserv. Biol. 18, 17–37.

Escalante, E.E., 1995. Coffee and agroforestry in Venezuela. Agrofor. today 7, 5–7.

Escamilla-Prado, E., Díaz-Cárdenas, S., 2002. Alternativas parasistemas de cultivo de café y su manejo en México, in: Pohlan, J. (Ed.), México y La Cafeticultura Chiapaneca: Reflexiones y Alternativas Para Los Caficultores. Shaker Verlag, Germany, pp. 125–154.

Escamilla-Prado, E., Landeros-Sánchez, C., 2016. Cafés diferenciados y de especialidad. Centro Nacional de Investigación, Innovación y Desarrollo Tecnológico de Café.

Feldpausch, T.R., Riha, S.J., Fernandes, E.C.M., Wandelli, E. V, 2005. Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. Earth Interact. 9, 1–22. https://doi.org/10.1175/EI140.1

Fernández, F., Sharkey, M.J., Sociedad Colombiana de Entomología., F., Universidad Nacional de Colombia., 2006. Introducción a los Hymenoptera de la región neotropical. Sociedad Colombiana de Entomología.

Fiedler, A.K., Landis, D.A., Wratten, S.D., 2008. Maximizing ecosystem services from conservation biological control: The role of habitat management. Biol. Control 45, 254–271. https://doi.org/10.1016/j.biocontrol.2007.12.009

Fonseca, M.M., Lima, E., Lemos, F., Venzon, M., Janssen, A., 2017. Non-crop plant to attract and conserve an aphid predator (Coleoptera: Coccinellidae) in tomato. Biol. Control 115, 129–134. https://doi.org/10.1016/j.biocontrol.2017.10.005

Frank, S.D., 2010. Biological control of arthropod pests using banker plant systems: Past progress and future directions. Biol. Control 52, 8–16. https://doi.org/10.1016/j.biocontrol.2009.09.011

Fraser, S.E.M., Dytham, C., Mayhew, P.J., 2007. Determinants of parasitoid abundance and diversity in woodland habitats. J. Appl. Ecol. 44, 352–361. https://doi.org/10.1111/j.1365-2664.2006.01266.x

Gómez Ruiz, J., Santos Ovilla, A., Valle-Mora, J., Montoya Gerardo, P.J., 2010. Determinación del establecimiento de parasitoides de la broca del café Hypothenemus hampei (Coleoptera: Curculionidae, Scolytinae) en cafetales del Soconusco, Chiapas, México. Entomotropica 25, 25–35.

González-Moreno, A., Bordera, S., Leirana-Alcocer, J., Delfín-González, H., Ballina-Gómez, H.S., 2018. Explaining variations in the diversity of parasitoid assemblages in a biosphere reserve of Mexico: Evidence from vegetation, land management and seasonality. Bull. Entomol. Res. 108, 602–615. https://doi.org/10.1017/S0007485317001134

Goulet, H., Huber, J., 1993. Hymenoptera of the World: An Identification Guide to Families, Ottawa: Agriculture Canada.

Gower, J.C., 1971. A General Coefficient of Similarity and Some of Its Properties. Biometrics 27, 857–871. https://doi.org/10.2307/2528823

Guharay, F., Monterrey M, J.A., Monterroso Salvatierra, D., Staver, C., 2000. Manejo integrado de plagas en el cultivo del café. Inf. técnico.

Guharay, F., Monterroso, D., Staver, C., 2001. El diseño y manejo de la sombra para la supresión de plagas en cafetales de América Central. Agroforestería en las Américas 8, 22–29.

Hajian-Forooshani, Z., Gonthier, D.J., Marín, L., Iverson, A.L., Perfecto, I., 2014. Changes in species diversity of arboreal spiders in Mexican coffee agroecosystems: untangling the web of local and landscape influences driving diversity. PeerJ 2, e623. https://doi.org/10.7717/peerj.623

Harterreiten-Souza, É.S., Togni, P.H.B., Pires, C.S.S., Sujii, E.R., 2014. The role of integrating agroforestry and vegetable planting in structuring communities of herbivorous insects and their natural enemies in the Neotropical region. Agrofor. Syst. 88, 205–219. https://doi.org/10.1007/s10457-013-9666-1

Herbst, C., Arnold-Schwandner, S., Meiners, T., Peters, M.K., Rothenwöhrer, C., Steckel, J., Wäschke, N., Westphal, C., Obermaier, E., 2017. Direct and indirect effects of agricultural intensification on a host-parasitoid system on the ribwort plantain (Plantago lanceolata L.) in a landscape context. Landsc. Ecol. 32, 2015–2028. https://doi.org/10.1007/s10980-017-0562-3

Herzog, F., 1994. Multipurpose shade trees in coffee and cocoa plantations in Côte d'Ivoire. Agrofor. Syst. 27, 259–267. https://doi.org/10.1007/BF00705060

Hochberg, M.E., Ives, A.R., 2000. Parasitoid Population Biology. USA, Princeton University Press.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT : an R package for rarefaction and extrapolation of species diversity (Hill numbers) 1451–1456. https://doi.org/10.1111/2041-210X.12613

Jha, S., Bacon, C.M., Philpott, S.M., MÉndez, V.E., LÄderach, P., Rice, R.A., 2014. Shade coffee: Update on a disappearing refuge for biodiversity. Bioscience 64, 416–428. https://doi.org/10.1093/biosci/biu038

Jonsson, M., Wratten, S.D., Landis, D.A., Gurr, G.M., 2008. Recent advances in conservation biological control of arthropods by arthropods. Biol. Control 45, 172–175. https://doi.org/10.1016/j.biocontrol.2008.01.006

Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv. Biol. 16, 1003–1014. https://doi.org/10.1046/j.1523-1739.2002.00499.x

Komar, O., 2006. Priority contribution. Ecology and conservation of birds in coffee plantations: A critical review. Bird Conserv. Int. 16, 1–23. https://doi.org/10.1017/S0959270906000074

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. Annu. Rev. Entomol. 45, 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

LaSalle, J., Gauld, I.D., 1993. Hymenoptera and biodiversity, Cabi Series. C.A.B. International.

Lassau, S.A., Hochuli, D.F., 2005. Wasp community responses to habitat complexity in Sydney sandstone forests. Austral Ecol. 30, 179–187. https://doi.org/10.1111/j.1442-9993.2005.01435.x

Lewis, C.N., Whitfield, J.B., 1999. Braconid wasp (hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. Environ. Entomol. 28, 986–997. https://doi.org/10.1093/ee/28.6.986

Liere, H., Jackson, D., Vandermeer, J., 2012. Ecological Complexity in a Coffee Agroecosystem: Spatial Heterogeneity, Population Persistence and Biological Control. PLoS One 7, 1–9. https://doi.org/10.1371/journal.pone.0045508

Liere, H., Jha, S., Philpott, S.M., 2017. Intersection between biodiversity conservation, agroecology, and ecosystem services. Agroecol. Sustain. Food Syst. 41, 723–760. https://doi.org/10.1080/21683565.2017.1330796

Lin, B.B., 2007. Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. Agric. For. Meteorol. 144, 85–94. https://doi.org/10.1016/j.agrformet.2006.12.009

Lomeli-Flores, J.R., Barrera, J.F., Bernal, J.S., 2009. Impact of natural enemies on Leucoptera coffeella (Lepidoptera: Lyonetiidae) population dynamics in Chiapas, Mexico. Biol. Control 51, 51–60. https://doi.org/10.1016/j.biocontrol.2009.03.021

Lomelí-Flores, J.R., Barrera, J.F., Bernal, J.S., 2010. Impacts of weather, shade cover and elevation on coffee leafminer Leucoptera coffeella (Lepidoptera: Lyonetiidae) population dynamics and natural enemies. Crop Prot. 29, 1039–1048. https://doi.org/10.1016/j.cropro.2010.03.007

López-Gómez, A.M., Williams-Linera, G., Manson, R.H., 2008. Tree species diversity and vegetation structure in shade coffee farms in Veracruz, Mexico. Agric. Ecosyst. Environ. 124, 160–172. https://doi.org/10.1016/j.agee.2007.09.008

López-Morgado, Rosalío, Escamilla-Prado, E., Díaz-Padilla, G., Guajardo-Panes, R.A., Martínez-Rodríguez, J.L., García-Mayoral, L.E., Castillo-Guerrero, M.C., López-Ramírez, M.A., Barreda-Ruiz, S., 2013. La cafeticultura en México y su problemática, in: López-Morgado, R., G., D.-P., Zamarripa-Colmenero, A. (Eds.), El Sistema Producto Café En México: Problemática y Tecnología de Producción. Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, México, pp. 5–31.

Mächler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2012. Cluster: Cluster Analysis Basics and Extensions.

Manson, R.H., Sosa-Fernández, V., 2019. Los cafetales mexicanos y su papel en la conservación de la biodiversidad y los servicios ecosistémicos, in: Bello-Baltazar, E., Soto-Pinto, L., Huerta-Palacios, G., Gómez-Ruiz, J. (Eds.), Caminar El Cafetal: Perspectivas Socioambientales Del Café y Su Gente. El Colegio de la Frontera Sur y Juan Pablos Editor, S.A., México, pp. 21–32.

Mariño, Y.A., Pérez, M.E., Gallardo, F., Trifilio, M., Cruz, M., Bayman, P., 2016. Sun vs. shade affects infestation, total population and sex ratio of the coffee berry borer (Hypothenemus hampei) in Puerto Rico. Agric. Ecosyst. Environ. 222, 258–266. https://doi.org/10.1016/j.agee.2015.12.031

Mas, A.H.., Dietsch, T. V., 2016. An Index of Management Intensity for Coffee Agroecosystems to Evaluate Butterfly Species Richness. Ecol. Appl. 13, 1491–1501.

Mazón, M., 2016. Taking shortcuts to measure species diversity: parasitoid Hymenoptera subfamilies as surrogates of species richness. Biodivers. Conserv. 25, 67–76. https://doi.org/10.1007/s10531-015-1029-y

McCune, B.P., Grace, J., 2002. Analysis of Ecological Communities, Journal of Experimental Marine Biology and Ecology - J EXP MAR BIOL ECOL. https://doi.org/10.1016/S0022-0981(03)00091-1

Méndez-López, I., Rodriguez-Bámaca, A., Sánchez-Huinaque, M.A., 2017. Metodología para la producción de plantas de café Robusta por estacas enraizadas. Claridades Agropecu. 14–15.

Mills, N.J., Jones, V.P., Baker, C.C., Melton, T.D., Steffan, S.A., Unruh, T.R., Horton, D.R., Shearer, P.W., Amarasekare, K.G., Milickzy, E., 2016. Using plant volatile traps to estimate the diversity of natural enemy communities in orchard ecosystems. Biol. Control 102, 66–76. https://doi.org/10.1016/j.biocontrol.2016.05.001

Miranda, F., 1998. La vegetación de Chiapas, 3ra ed. Consejo Estatal para la Cultura y las Artes de Chiapas, Tuxtla Gutiérrez, Chiapas, México.

Moguel, P., Toledo, V., 1996. El café en México, ecología, cultura indígena y sustentabilidad. Ciencias 40–51.

Moguel, P., Toledo, V.M., 1999. Biodiversity conservation in tradicional Coffee systems of Mexico. Conserv. Biol. 13, 11–21. https://doi.org/10.1046/j.1523-1739.1999.97153.x

Monterrey, J., Suárez, D., González, M., 2001. Comportamiento de insectos en sistemas agroforestales con café en el Pacífico Sur de Nicaragua. Agroforestería en las américas 8, 15–21.

Muschler, R.G., 2006. Manejo de sombra para cafetales sostenibles, in: Pohlan, J., Soto, L., Barrera, J. (Eds.), El Cafetal Del Futuro: Realidades y Visiones. Shaker Verlag, Germany, pp. 39–62.

Nestel, D., Dickschen, F., Altieri, M.A., 1994. Seasonal and spatial population loads of a tropical insect: the case of the coffee leaf-miner in Mexico. Ecol. Entomol. 19, 159–167. https://doi.org/10.1111/j.1365-2311.1994.tb00406.x

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package.

Pak, D., Iverson, A.L., Ennis, K.K., Gonthier, D.J., Vandermeer, J.H., 2015. Parasitoid wasps benefit from shade tree size and landscape complexity in Mexican coffee agroecosystems. Agric. Ecosyst. Environ. 206, 21–32. https://doi.org/10.1016/j.agee.2015.03.017

Peeters, L.Y.K., Soto-Pinto, L., Perales, H., Montoya, G., Ishiki, M., 2003. Coffee production, timber, and firewood in traditional and Inga-shaded plantations in Southern Mexico. Agric. Ecosyst. Environ. 95, 481–493. https://doi.org/10.1016/S0167-8809(02)00204-9

Pereira, E.J.G., Picanço, M.C., Bacci, L., Crespo, A.L.B., Guedes, R.N.C., 2007. Seasonal mortality factors of the coffee leafminer, Leucoptera coffeella. Bull. Entomol. Res. 97, 421–432. https://doi.org/10.1017/S0007485307005202

Perfecto, I., Rice, R.A., Greenberg, R., van der Voort, M.E., 1996. Shade Coffee: A Disappearing Refuge for Biodiversity. Bioscience 46, 598–608. https://doi.org/10.2307/1312989

Perfecto, I., Vandermeer, J., 2015. Coffee agroecology: A new approach to unferstanding agricultural biodiversity, ecosystem services and sustainable development. Routledge, London, UK.

Perfecto, I., Vandermeer, J., Carti, V., 1997. Arthropod biodiversity loss and the trans formation of a tropical agro-ecosystem. Biodivers. Conserv. 945, 935–945. https://doi.org/10.1023/A:1018359429106

Perfecto, I., Vandermeer, J., Philpott, S.M., 2010. Complejidad ecológica y el control de plagas en un cafetal orgánico: Develando un servicio ecosistémico autónomo. Agroecología 5, 41–51.

Philpott, S.M., Arendt, W.J., Armbrecht, I., Bichier, P., Diestch, T. V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., Tejeda-Cruz, C., Williams-Linera, G., Valenzuela, J., Zolotoff, J.M., 2008. Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. Conserv. Biol. 22, 1093–1105. https://doi.org/10.1111/j.1523-1739.2008.01029.x

R Core Team, 2018. R: A language and environment for statistical computing.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Fay, J.P., 2001. Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats. Conserv. Biol. 15, 378–388. https://doi.org/10.1046/j.1523-1739.2001.015002378.x

Righi, C.A., Campoe, O.C., Bernardes, M.S., Lunz, A.M.P., Piedade, S.M.S., Pereira, C.R., 2013. Influence of rubber trees on leaf-miner damage to coffee plants in an agroforestry system. Agrofor. Syst. 87, 1351–1362. https://doi.org/10.1007/s10457-

013-9642-9

Rodríguez, J.M., Rodríguez-Velez, B., Zaragoza-Caballero, S., Noguera-Martínez, F.A., González-Soriano, E., Ramírez-García, E., 2010. Diversity of encyrtidae (Hymenoptera: Chalcidoidea) collected with Malaise traps in the tropical dry forest of San Javier, Sonora, Mexico. Rev. Mex. Biodivers. 81, 813–822.

Romero-Alvarado, Y., Soto-Pinto, L., García-Barrios, L., Barrera-Gaytán, J.F., 2002. Coffee yields and soil nutrients under the shades of Inga sp. vs. multiple species in Chiapas, Mexico. Agrofor. Syst. 54, 215–224. https://doi.org/10.1023/A:1016013730154

Shapiro, B.A., Pickering, J., 2000. Rainfall and parasitic wasp (Hymenoptera: Ichneumonoidea) activity in successional forest stages at Barro Colorado Nature Monument, Panama, and La Selva Biological Station, Costa Rica. Agric. For. Entomol. 2, 39–47. https://doi.org/10.1046/j.1461-9563.2000.00048.x

Sosa-Aranda, I., del-Val, E., Hernández-Martínez, G., Arroyo-Lambaer, D., Uscanga, A., Boege, K., 2018. Response of lepidopteran herbivore communities to crop management in coffee plantations. Agric. Ecosyst. Environ. 265, 37–44. https://doi.org/10.1016/j.agee.2018.05.018

Soto-Pinto, L., 2002. Interacciones entre la sombra, la producción y la salud del sistema, in: Pohlan, J. (Ed.), México y La Cafeticultura Chiapaneca: Reflexiones y Alternativas Para Los Caficultores. Shaker Verlag, Germany, pp. 119–124.

Sperber, C.F., Nakayama, K., Valverde, M.J., De Siqueira Neves, F., 2004. Tree species richness and density affect parasitoid diversity in cacao agroforestry. Basic Appl. Ecol. 5, 241–251. https://doi.org/10.1016/j.baae.2004.04.001

Staver, C., Juventia, S., Navarrete, E., Navarrete, L., Sepulveda, N., Barrios, M., 2020. Long-term response of groundcover components to organic and conventional weed control in shaded and open-sun coffee in Nicaragua. Crop Prot. 133, 105150. https://doi.org/10.1016/j.cropro.2020.105150

Teodoro, A., Klein, A.M., Tscharntke, T., 2008. Environmentally mediated coffee pest densities in relation to agroforestry management, using hierarchical partitioning analyses. Agric. Ecosyst. Environ. 125, 120–126. https://doi.org/10.1016/j.agee.2007.12.004

Tscharntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes - A review. J. Appl. Ecol. https://doi.org/10.1111/j.1365-2664.2010.01939.x

Tylianakis, J., Klein, A., Tscharntke, T., 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. Ecology 86, 3296–3302.

Villacorta, A., 1980. Alguns fatores que afetam a populacao estacional de (Perileucoptera coffeella) Guérin-Méneville, 1842 (Lepidoptera:Lyonetiidae) no norte do Paraná. An. da Soc. Entomol. do Bras. 9, 23–32.

Wolda, H., 1992. Trends in abundance of tropical forest insects. Oecologia 89, 47–52.

https://doi.org/10.1007/BF00319014

Wolda, H., 1988. Insect seasonality: why? Annu. Rev. Ecol. Syst. Vol. 19 1–18. https://doi.org/10.1146/annurev.es.19.110188.000245

Wyckhuys, K.A.G., Lu, Y., Morales, H., Vázquez, L.L., Legaspi, J., Eliopoulos, P., Hernandez, L., 2013. Current status and potential of conservation biological control for agriculture in the developing world. Biol. Control 65, 152–167. https://doi.org/10.1016/j.biocontrol.2012.11.010

Young, A.M., 1982. Population Biology of Tropical Insects. Springer US, Boston, MA. https://doi.org/10.1007/978-1-4684-1113-3

## Figure legends

**Figure 1.** Parasitoid species accumulation graphs. a) Total or grouped, b) per season of the year, and c) per management intensity, based on Hill's numbers, q=0 (left), q=1 (center) and q=2 (right). The shaded regions represent 95% confidence intervals, the solid lines represent the samples obtained in field and the dashed lines represent the estimation through the extrapolation method.

**Figure 2.** Comparison of the parasitoid average abundance (± SE) between: a) collecting seasons, and b) management intensities, based on Kruskal-Wallis's test.

**Figure 3.** Average (± SE) of the most abundant parasitoid families and comparisons between them during collecting seasons and management intensity, based on the Kruskal-Wallis's test ($P < 0.05$).

**Figure 4.** Average (± SE) of parasitoids divided in families with the most richness, and comparisons between the collecting seasons and management intensities, based on the Kruskal-Wallis's test ($P < 0.05$).

**Figure 5.** nMDS ordination graphs, grouping experimental plots in: a) management intensity, b) shading tree coverage, c) shading tree richness, and d) presence or absence of fruit trees.

**Figure 6.** Triplot made out of the nMDS ordination of robusta coffee experimental plots and grouped per their management intensity. Ellipses showcase the 95% confidence intervals around the different plot management centroids. The stress value indicates the goodness-of-fit of the ordination representation. The recorded quantitative variables that

turned out to be significant are shown through arrows, where the vector distance states the variable intensity. Age of plantations, altitude (Alt), richness (STR) and shading coverage (ShC), herb coverage (HC), leaf litter (LL) and bare ground (BG) coverage. The parasitoid families correlated to the ordination were: Cera = Ceraphronidae, Diap = Diapriidae, Ency = Encyrtidae, Ichn = Ichneumonidae, Myma = Mymaridae, Tric = Trichogrammatidae.

**Figure 7**. Average percentage (± SE) of significant pest incidence during the two collecting seasons and the three management intensities of robusta coffee plots. a) Damaged leaves by the coffee leaf miner (*L. coffeella*), b) leaves with insect herbivory, and c) berries bored by the coffee borer (*H. hampei*). The means with different letters are significantly different to $P < 0.05$, according to the Kruskal Wallis's test.

## Supplementary Material

**Figure S1.** Monthly rainfall (mm) recorded at the Alianza coffee farm (Soconusco region, Chiapas, Mexico) from January to August, 2019.

## Tables

**Table 1**. Categorization of robusta coffee experimental plots per agronomic management intensity. Soconusco region, Chiapas, Mexico. 2019.

| Agronomic management | Low-intensity management (n = 4) | Moderate management (n = 12) | Intense management (n = 8) |
|---|---|---|---|
| Cultivation management labor | Routine pruning practices with machete | Routine pruning practices with machete | Routine pruning practices with machete |
| Soil fertilization and conservation | Use of organic compost or waste product of pruning and activities inside the plots | Use of organic compost or waste product of pruning and activities inside the plots, in addition to the use of inorganic fertilizers at least once a year | Frequent usage of inorganic fertilizers (three times a year or more) |
| Weed management | Removal of weed with machete | Removal of weed with machete and at least one use of herbicides a year | Removal of weed with machete and regular usage of chemical products to control weed |
| Disease management | None | Occasional use of fungicides | None |

| Pest management | Coffee berry borer traps, sanitary pruning | Coffee berry borer traps, sanitary pruning | Coffee berry borer traps, sanitary pruning, and preventive use of insecticides |
|---|---|---|---|
| Plantation age (years) | 10.7 ± 1.0 **a *** | 9.1 ± 0.3 **ab** | 7.7 ± 0.5 **b** |
| Altitude (masl) | 506.5 ± 21.2 **a** | 498.5 ± 3.0 **a** | 714.6 ± 4.4 **b** |
| Shade coverage (%) | 75.3 ± 4.8 **a** | 50.9 ± 3.4 **b** | 15.4 ± 4.2 **c** |
| Shading tree richness (number of trees) | 4.2 ± 0.4 **a** | 2.8 ± 0.2 **b** | 0.6 ± 0.1 **c** |
| Herb coverage (%) | 37.5 ± 5.2 **ab** | 27.0 ± 2.9 **b** | 49.1 ± 6.0 **a** |
| Leaf litter (%) | 53.7 ± 6.2 **a** | 64.7 ± 2.8 **a** | 34.5 ± 4.8 **b** |
| Bare ground (%) | 8.7 ± 2.9 **ab** | 8.1 ± 1.6 **b** | 15.8 ± 2.9 **a** |

* Average values (± SE) and the Kruskal-Wallis test for comparisons between management intensities, in which the different letters show significant differences amongst the management categories ($P < 0.05$).

**Table 2**. Abundance and richness of families of parasitoid wasps collected in robusta coffee plots under three management intensities during two collecting seasons. Soconusco region, Chiapas, Mexico. 2019

| Families | Season $^{1}$ | | Management intensity | | | | | | | | | Total | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | D | R | Low | | | Moderate | | | Intense | | | Abundance | | Richness | |
| | | | D | R | T | D | R | T | D | R | T | I | % | MS | % |
| Agaonidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0.04 | 1 | 0.43 |
| Aphelinidae | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 3 | 0.13 | 2 | 0.87 |
| Bethylidae | 19 | 16 | 6 | 2 | 8 | 5 | 6 | 11 | 8 | 8 | 16 | 35 | 1.48 | 8 | 3.48 |
| Braconidae | 59 | 82 | 8 | 11 | 19 | 30 | 61 | 91 | 21 | 10 | 31 | 141 | 5.96 | 20 | 8.70 |
| Ceraphronidae | 311 | 39 | 63 | 8 | 71 | 206 | 12 | 218 | 42 | 19 | 61 | 350 | 14.80 | 6 | 2.61 |
| Chalcididae | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0.04 | 1 | 0.43 |
| Diapriidae | 402 | 185 | 113 | 27 | 140 | 213 | 117 | 330 | 76 | 41 | 117 | 587 | 24.82 | 12 | 5.22 |
| Dryinidae | 32 | 9 | 6 | 3 | 9 | 15 | 5 | 20 | 11 | 1 | 12 | 41 | 1.73 | 11 | 4.78 |
| Embolemidae | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0.04 | 1 | 0.43 |
| Encyrtidae | 269 | 168 | 8 | 8 | 16 | 53 | 89 | 142 | 208 | 71 | 279 | 437 | 18.48 | 22 | 9.57 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eucharitidae | 0 | 9 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 7 | 7 | 9 | 0.38 | 2 | 0.87 |
| Eulophidae | 27 | 10 | 9 | 1 | 10 | 8 | 4 | 12 | 10 | 5 | 15 | 37 | 1.56 | 13 | 5.65 |
| Eupelmidae | 4 | 2 | 0 | 0 | 0 | 4 | 1 | 5 | 0 | 1 | 1 | 6 | 0.25 | 4 | 1.74 |
| Eurytomidae | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 3 | 0.13 | 2 | 0.87 |
| Evaniidae | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0.08 | 1 | 0.43 |
| Figitidae | 8 | 22 | 1 | 8 | 9 | 2 | 9 | 11 | 5 | 5 | 10 | 30 | 1.27 | 12 | 5.22 |
| Ichneumo[2] | 16 | 43 | 0 | 7 | 7 | 7 | 19 | 26 | 9 | 17 | 26 | 59 | 2.49 | 22 | 9.57 |
| Mymaridae | 57 | 29 | 5 | 6 | 11 | 15 | 7 | 22 | 37 | 16 | 53 | 86 | 3.64 | 20 | 8.70 |
| Platygastridae | 49 | 46 | 9 | 7 | 16 | 12 | 7 | 19 | 28 | 32 | 60 | 95 | 4.02 | 8 | 3.48 |
| Proctotrupidae | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 4 | 0.17 | 1 | 0.43 |
| Pteromalidae | 62 | 44 | 8 | 0 | 8 | 37 | 34 | 71 | 17 | 10 | 27 | 106 | 4.48 | 17 | 7.39 |
| Scelionidae | 164 | 125 | 52 | 22 | 74 | 63 | 51 | 114 | 49 | 52 | 101 | 289 | 12.22 | 28 | 12.17 |
| Signiphoridae | 4 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 3 | 5 | 0.21 | 4 | 1.74 |
| Torymidae | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.04 | 1 | 0.43 |
| Trichogram[3] | 31 | 5 | 2 | 0 | 2 | 5 | 0 | 5 | 24 | 5 | 29 | 36 | 1.52 | 11 | 4.78 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total | 1521 | 844 | 292 | 113 | 405 | 677 | 428 | 1105 | 552 | 303 | 855 | 2365 | 100% | 230 | 100% |

[1] D= dry, R= rainy, T= total; [2] Ichneumo= Ichneumonidae; [3] Trichogram= Trichogrammatidae.

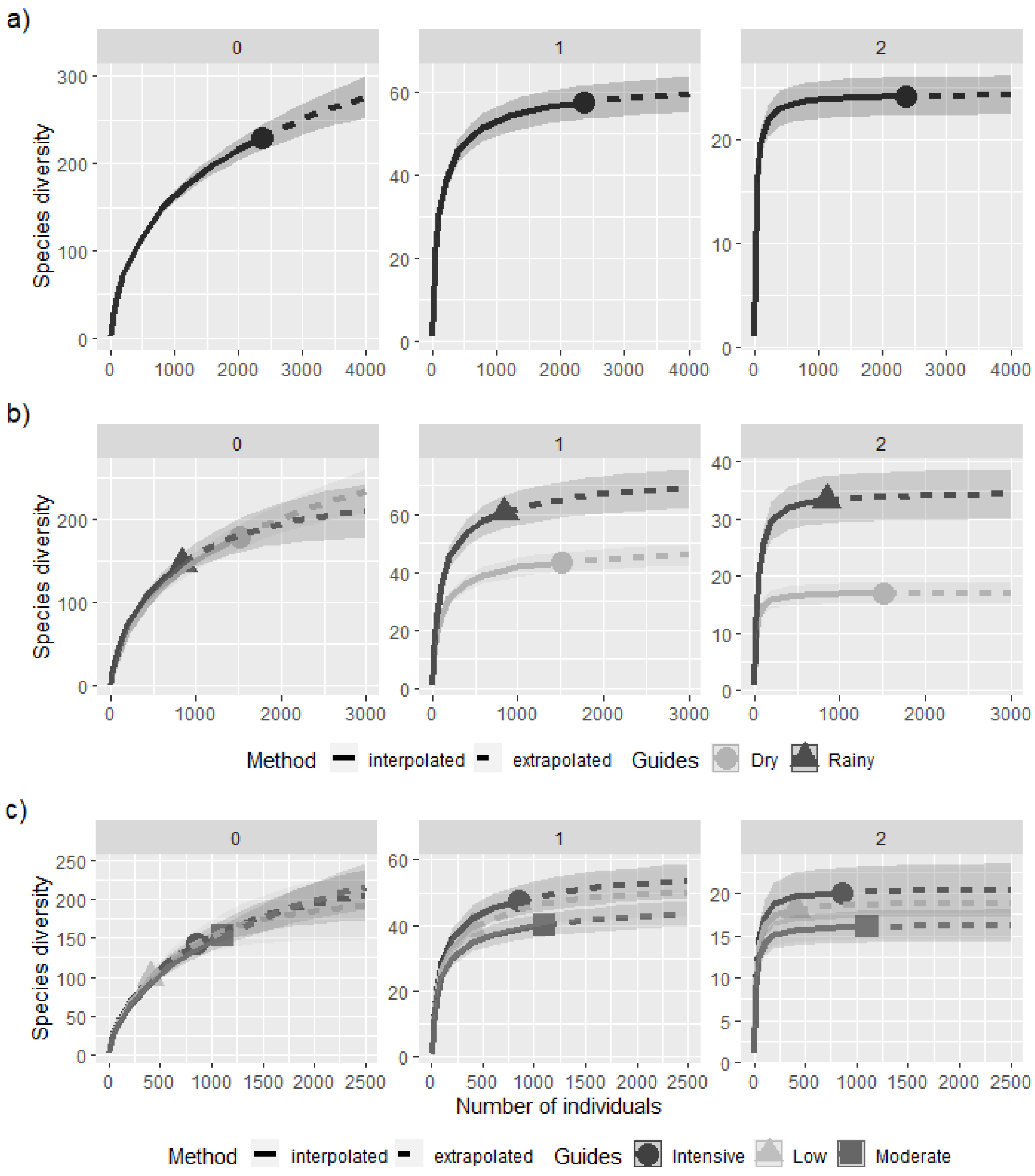
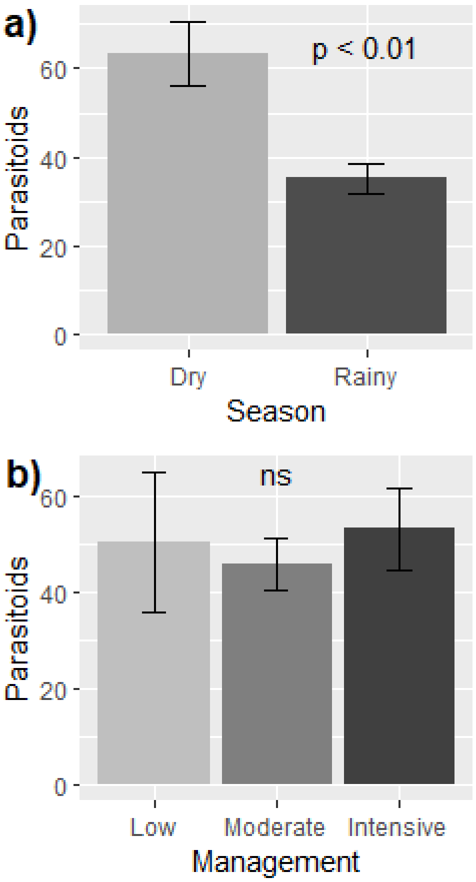

a)
0
1
2
Species diversity
300
200
100
0
60
40
20
0
20
10
0
0
1000
2000
3000
4000
b)
Species diversity
200
100
40
30
0
1000
2000
3000
Method
interpolated
extrapolated
Guides
Dry
Rainy
c)
Species diversity
250
200
150
100
50
15
5
500
1500
2500
Number of individuals
Method
interpolated
extrapolated
Guides
Intensive
Low
Moderate

**Figure 1.**


a)
p < 0.01
Parasitoids
60
40
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Dry
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Season
b)
ns
Parasitoids
60
40
20
0
Low
Moderate
Intensive
Management

**Figure 2.**

**Figure 3.**

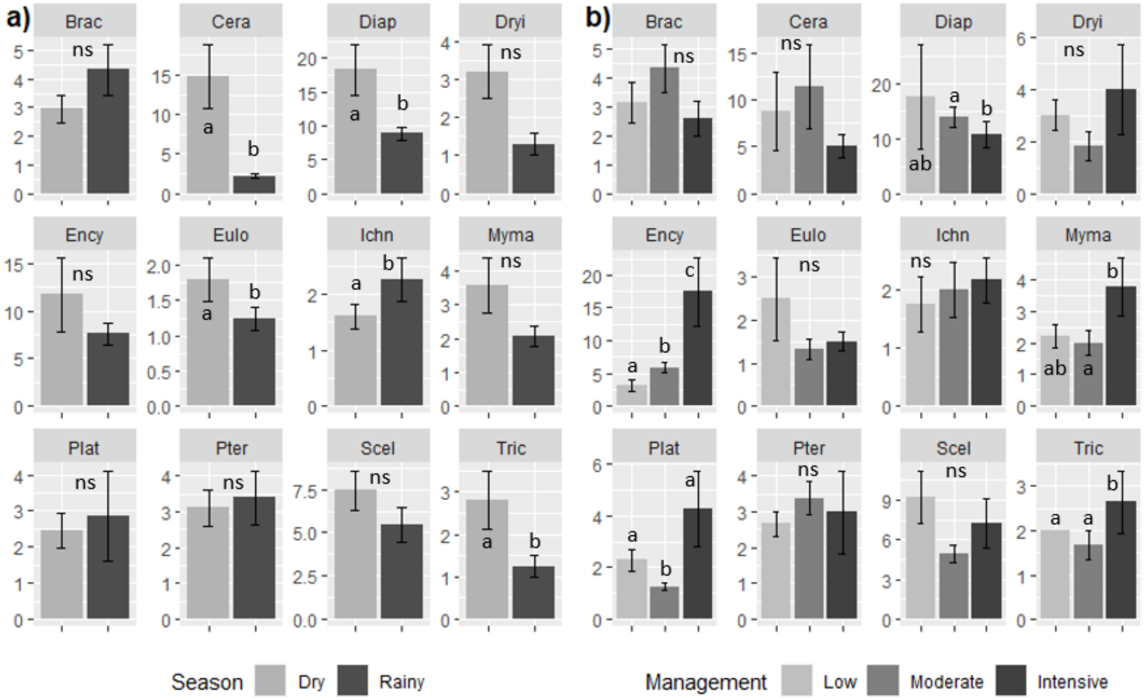
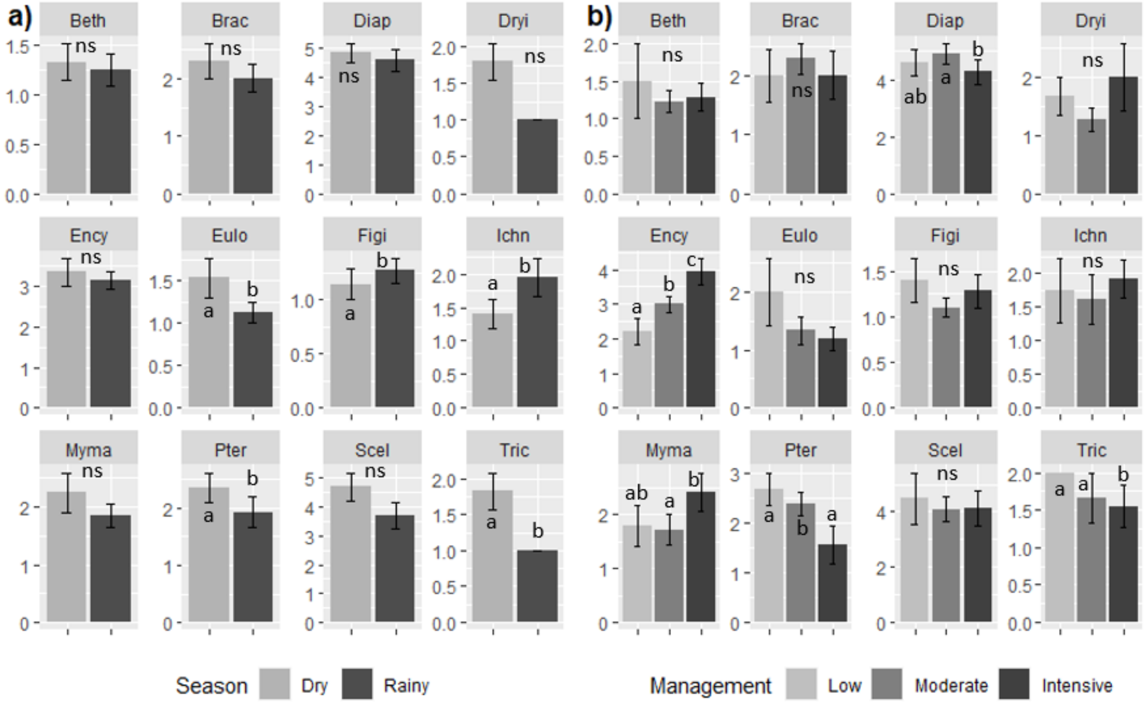


**Figure 4.**



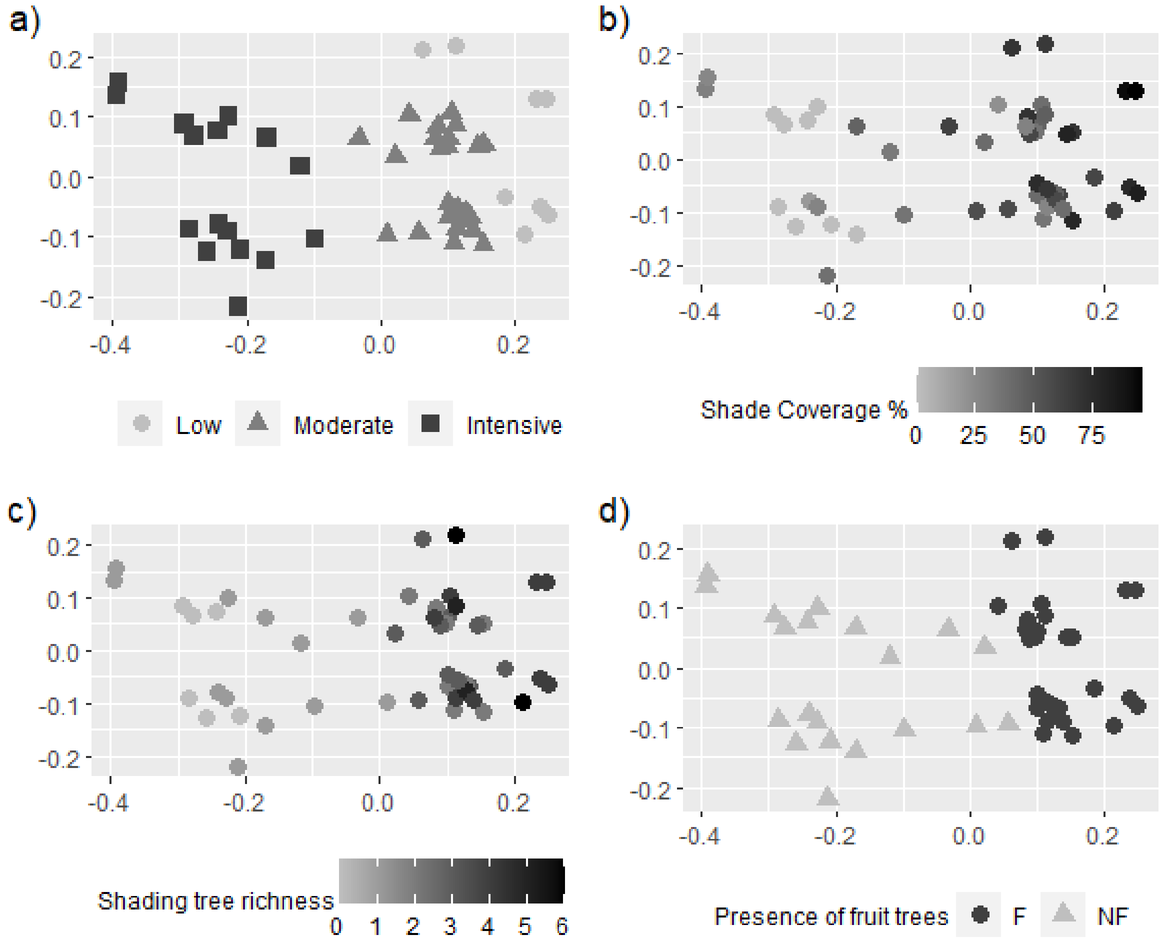

a)
0.2
0.1
0.0
-0.1
-0.2
-0.4
-0.2
0.0
0.2
Low
Moderate
Intensive
b)
Shade Coverage %
0
25
50
75
c)
Shading tree richness
0
1
2
3
4
5
6
d)
Presence of fruit trees
F
NF

**Figure 5.**

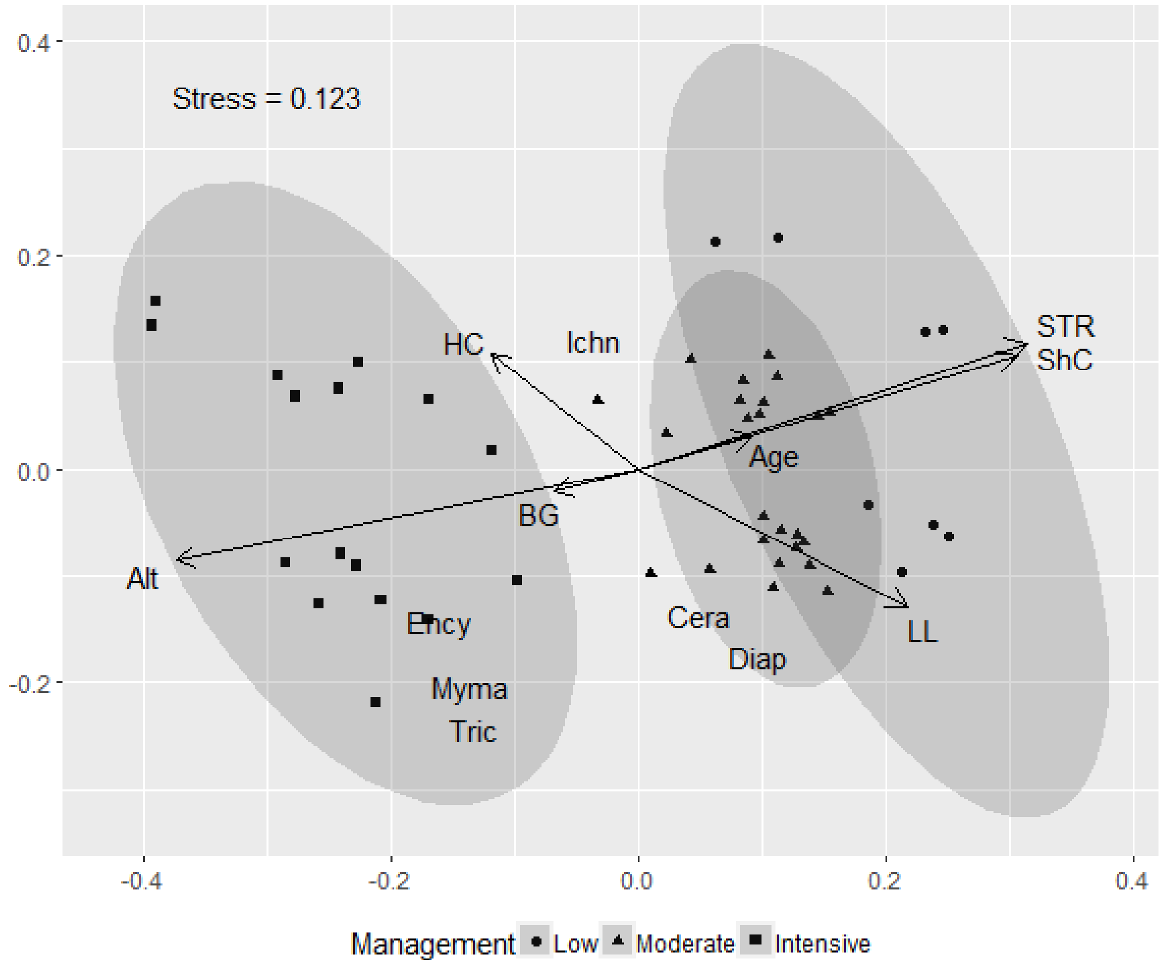
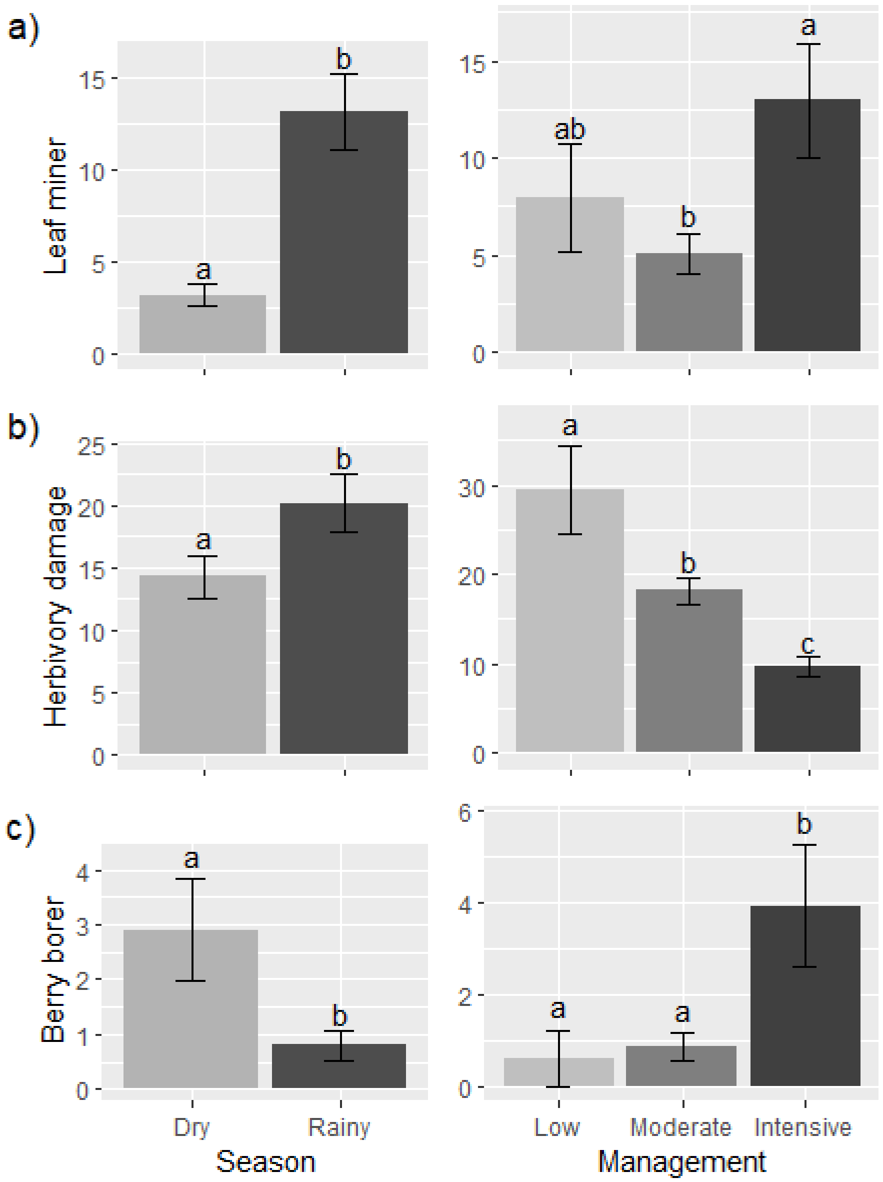

Stress = 0.123
0.4
0.2
0.0
-0.2
-0.4
-0.2
0.0
0.2
0.4
HC
Ichn
STR
ShC
Age
BG
Alt
Ency
Myma
Tric
Cera
Diap
LL
Management
● Low
▲ Moderate
■ Intensive

**Figure 6.**



a)
Leaf miner
15
10
5
0
a
b
15
10
5
0
ab
b
a
b)
Herbivory damage
25
20
15
10
5
0
a
b
30
20
10
0
a
b
c
c)
Berry borer
4
3
2
1
0
a
b
6
4
2
0
a
a
b
Dry
Rainy
Season
Low
Moderate
Intensive
Management

**Figure 7.**

## Supplementary Material-Tables

**Table S1.** Shade trees found in 24 robusta coffee experimental plots

| Scientific name | Common name | Family | Tree type | Plot management | | | Frequency | |
|---|---|---|---|---|---|---|---|---|
| | | | | L | M | I | No. | % |
| *Annona muricata* | Guanabana | Annonaceae | F | + | | | 2 | 8.3 |
| *Aspidosperma megalocarpon* | Chiche | Apocynaceae | NF | + | + | | 6 | 25.0 |
| *Cedrela odorata* | Cedar | Meliaceae | NF | | + | | 1 | 4.2 |
| *Ceiba pentandra* | Ceiba | Malvaceae | NF | | + | | 2 | 8.3 |
| *Citrus × sinensis* | Orange | Rutaceae | F | + | | | 1 | 4.2 |
| *Citrus × tangerina* | Tangerine | Rutaceae | F | + | | | 3 | 12.5 |
| *Hevea brasiliensis* | Rubber Tree | Euphorbiaceae | NF | | | + | 2 | 8.3 |
| *Inga* spp. | Chalum | Fabaceae | NF | | + | + | 9 | 37.5 |
| *Mangifera indica* | Mango | Anacardiaceae | F | + | | | 1 | 4.2 |
| *Musa* spp. | Banana | Musaceae | F | | + | | 6 | 25.0 |
| *Nephelium lappaceum* | Rambutan | Sapindaceae | F | + | | | 3 | 12.5 |
| *Pouteria sapota* | Mamey | Sapotaceae | F | + | + | | 5 | 20.8 |
| *Ricinus communis* | Higuerilla | Euphorbiaceae | NF | | + | | 1 | 4.2 |
| *Tabebuia donnell-smithii* | Primavera | Bignoniaceae | NF | + | + | | 4 | 16.7 |
| *Terminalia amazonia* | Flying Guava | Combretaceae | NF | | | + | 3 | 12.5 |
| *Theobroma cacao* | Cocoa | Malvaceae | NF | | + | | 6 | 25.0 |
| *Trema micrantha* | Maroon Capulin | Cannabaceae | NF | + | + | | 2 | 8.3 |

**Table S2.** Association between Non-metric multidimensional scaling (nMDS) arrangement with parasitoid wasp families

| Parasitoid wasp families | Key | $r^2$ | Pr(>r) |
|---|---|---|---|
| Agaonidae | Agao | 0.0095 | 0.927 |
| Aphelinidae | Aphe | 0.0168 | 0.697 |
| Bethylidae | Beth | 0.0174 | 0.69 |
| Braconidae | Brac | 0.0525 | 0.300 |
| Ceraphronidae | Cera | 0.1452 | 0.025 |
| Chalcididae | Chal | 0.0183 | 0.770 |
| Diapriidae | Diap | 0.193 | 0.007 |
| Dryinidae | Dryi | 0.0694 | 0.193 |
| Embolemidae | Embo | 0.0339 | 0.491 |
| Encyrtidae | Ency | 0.2177 | 0.003 |
| Eucharitidae | Euch | 0.0218 | 0.674 |
| Eulophidae | Eulo | 0.0814 | 0.150 |
| Eupelmidae | Eupe | 0.0158 | 0.748 |
| Eurytomidae | Eury | 0.0033 | 0.939 |
| Evaniidae | Evan | 0.0691 | 0.200 |
| Figitidae | Figi | 0.109 | 0.056 |
| Ichneumonidae | Ichn | 0.1454 | 0.030 |
| Mymaridae | Myma | 0.2589 | 0.002 |
| Platygastridae | Plat | 0.0711 | 0.163 |
| Proctotrupidae | Proc | 0.0227 | 0.629 |
| Pteromalidae | Pter | 0.1037 | 0.073 |
| Scelionidae | Scel | 0.0434 | 0.378 |
| Signiphoridae | Sign | 0.1275 | 0.043 |
| Torymidae | Tory | 0.0701 | 0.162 |
| Trichogrammatidae | Tric | 0.3009 | 0.002 |

**Table S3.** Association between Non-metric multidimensional scaling (nMDS) arrangement with environmental variables

| Variables | Key | $r^2$ | *P*(>r) |
|---|---|---|---|
| Continuous | | | |
| Plantation age | | 0.1804 | 0.014 |
| Shade Tree Richness | STR | 0.6671 | 0.001 |
| Shade Coverage (%) | ShC | 0.6541 | 0.001 |
| Altitude (masl) | | 0.7625 | 0.001 |
| Herb coverage (%) | CH | 0.3167 | 0.001 |
| Leaf litter (%) | LL | 0.504 | 0.001 |
| Bare ground (%) | BG | 0.1443 | 0.029 |
| Categorical | | | |
| Sampling Season | | 0.2046 | 0.001 |
| Management Intensity | | 0.6847 | 0.001 |
| Tree Type (F/NF) | | 0.5793 | 0.001 |

**Table S4.** Analysis of variance of the general linear model analysis (GLMs) for herbivore species associated with coffee in relation to parasitoid wasps, sampling season, management intensity and environmental variables.

| Herbivore species / Variables | LR Chisq | df | *P*(>Chisq) |
|---|---|---|---|
| Damage by Coffee Leaf Miner | | | |
| Parasitoid abundance | 8.050 | 1 | 0.0046 |
| Parasitoid richness | 12.529 | 1 | 0.0004 |
| Parasitoid Shannon diversity | 9.514 | 1 | 0.0020 |
| Sampling season | 114.129 | 1 | 0.0000 |
| Management intensity | 8.802 | 2 | 0.0123 |
| Age of the plantation | 5.135 | 1 | 0.0234 |
| Shade coverage | 0.261 | 1 | 0.6091 |
| Tree richness | 0.077 | 1 | 0.7818 |
| Presence of fruit trees | 0.753 | 1 | 0.3856 |
| Altitude | 16.947 | 1 | 0.0000 |
| Herb coverage | 0.036 | 1 | 0.8487 |
| Leaf litter coverage | 0.024 | 1 | 0.8774 |
| Bare ground | 0.310 | 1 | 0.5778 |
| | | | |
| Leaves with insect herbivory | | | |
| Parasitoid abundance | 1.113 | 1 | 0.2913 |
| Parasitoid richness | 0.276 | 1 | 0.5993 |
| Parasitoid Shannon diversity | 0.072 | 1 | 0.7883 |
| Sampling season | 26.809 | 1 | 0.0000 |
| Management intensity | 19.719 | 2 | 0.0000 |
| Age of the plantation | 0.670 | 1 | 0.4129 |
| Shade coverage | 0.063 | 1 | 0.8017 |
| Tree richness | 0.060 | 1 | 0.8067 |
| Presence of fruit trees | 3.710 | 1 | 0.0541 |
| Altitude | 11.538 | 1 | 0.0007 |
| Herb coverage | 2.430 | 1 | 0.1191 |
| Leaf litter coverage | 2.872 | 1 | 0.0901 |
| Bare ground | 2.327 | 1 | 0.1272 |
| | | | |
| Bored berries by Coffee Berry Borer | | | |
| Parasitoid abundance | 6.629 | 1 | 0.0100 |
| Parasitoid richness | 9.574 | 1 | 0.0020 |
| Parasitoid Shannon diversity | 7.964 | 1 | 0.0046 |
| Sampling season | 33.891 | 1 | 0.0000 |
| Management Intensity | 10.280 | 2 | 0.0059 |
| Age of the plantation | 0.531 | 1 | 0.4662 |
| Shade coverage | 0.817 | 1 | 0.3660 |
| Tree richness | 0.568 | 1 | 0.4509 |

| | | | |
|---|---|---|---|
| Presence of fruit trees | 1.627 | 1 | 0.2021 |
| Altitude | 0.243 | 1 | 0.6219 |
| Herb coverage | 1.810 | 1 | 0.1785 |
| Leaf litter coverage | 1.388 | 1 | 0.2388 |
| Bare ground | 2.083 | 1 | 0.1489 |

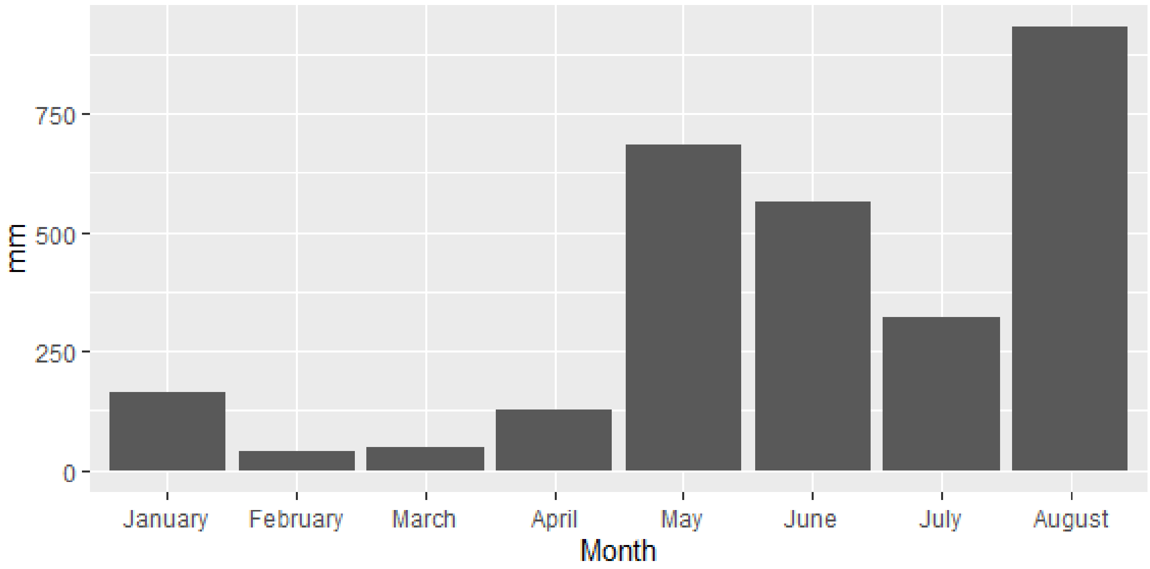


**Figure S1.**

# III. Conclusiones

En cuanto a la cobertura y riqueza de la sombra, los resultados indicaron que los valores de estas variables fueron significativamente menores conforme se intensificó el manejo. Podemos afirmar que las plantaciones con una intensidad baja y moderada son ricos en especies de árboles, no obstante, la modernización está alterando este sistema agroforestal disminuyendo la diversidad de árboles de sombra. La cobertura del suelo también fue afectada por la intensidad de manejo. Se encontró mayor presencia de cobertura de hojarasca en las parcelas de baja y moderada intensidad de manejo porque en éstas la cobertura y riqueza de la sombra fue mayor. Sin embargo, en nuestro estudio no se presentaron diferencias entre manejo bajo y manejo intensivo con respecto a la cobertura herbácea y suelo desnudo.

En total se registraron 230 morfoespecies de avispas parasitoides representadas en 25 familias. Diapriidae (587 individuos, 24.8 %), Encyrtidae (437 individuos, 18.5 %), Ceraphronidae (350 individuos, 14.8 %) y Scelionidae (289 individuos, 12.2 %) fueron las familias más abundantes. La mayor riqueza de avispas parasitoides se encontró en la temporada lluviosa, mientras que la abundancia de parasitoides fue mayor en la temporada seca. Sin embargo, no se encontraron diferencias significativas entre los tres niveles de intensidades de manejo sobre el total de la abundancia y riqueza de avispas parasitoides.

Por otro lado, se observaron cambios en la abundancia de algunas familias según la temporada del año. Diapriidae, Ceraphronidae, Eulophidae y Trichogrammatidae fueron más abundantes en la temporada seca, mientras que Ichneumonidae fue más abundante en la temporada lluviosa que en la seca. La abundancia de parasitoides mostró diferentes respuestas por familia. En cuanto a la riqueza de morfoespecies, Eulophidae, Pteromalidae y Trichogrammatidae presentaron mayor riqueza en la temporada seca y Figitidae e Ichneumonidae en la temporada lluviosa.

Nuestro estudio revela que las plantaciones de *C. canephora* comparten similitudes en cuanto a la composición de familias en plantaciones de café arábica (*C. arabica*) (Pak et al. 2015), e incluso, otros sistemas agroforestales como el del cacao (*Theobroma cacao*

L.) (Sperber et al. 2004; Mazón 2016), lo que sugiere que ambos sistemas agroforestales poseen una composición parasitoide similar.

Por otro lado, nuestros resultados evidencian que, dependiendo de las estrategias en las prácticas de manejo agrícola a un nivel local, puede promover o reducir la presencia de algunos grupos taxonómicos de avispas parasitoides. En este sentido, encontramos que las familias Encyrtidae, Mymaridae y Trichogrammatidae se asocian a las parcelas con manejo intensivo, mientras que Ceraphronidae y Diapriidae se asocian con parcelas sometidas a un manejo moderado. Por ello, la conservación de avispas parasitoides con fines de control biológico deberá tomar en cuenta múltiples factores, como el nivel de intensificación, el manejo de la cobertura y diversidad de la vegetación, la temporada del año y los grupos taxonómicos de los parasitoides involucrados.

El manejo, la temporada y la presencia de parasitoides tuvieron un efecto significativo sobre algunas plagas del café. Nuestros resultados indican que el daño a las hojas por *L. coffella* está relacionado con la temporada del año, el manejo y las avispas parasitoides. El daño fue mayor en la temporada lluviosa, lo cual concuerda con Lomeli-Flores et al. (2009; 2010) para la misma región. También el daño fue mayor en el manejo intensivo con respecto al moderado. En general, el daño del minador puede considerarse bajo y esto puede deberse a múltiples factores de mortalidad incluyendo los parasitoides (Guharay et al. 2001; Monterrey et al. 2001; Lomeli-Flores et al. 2009).

La herbivoría disminuyó conforme se intensificó el manejo de las parcelas experimentales y fue significativamente mayor en la temporada lluviosa. Estos resultados contrastan con Sosa-Aranda et al., (2018) quienes reportaron que las plantaciones de café con bajo índice de manejo tuvieron un porcentaje de daño foliar significativamente menor que las plantaciones con un manejo más intensivo. Por otra parte, la hipótesis de que los parasitoides tienen un efecto en la herbivoría no se confirma pues no se halló una asociación significativa con estos insectos.

Aunque varios autores reportan que la sombra favorece las infestaciones de broca del café (Teodoro et al. 2008; Bosselmann et al. 2009; Mariño et al. 2016), nuestros datos contradicen esta afirmación, pues encontramos que la infestación por broca fue menor durante la temporada lluviosa. También observamos un mayor porcentaje de frutos perforados en las parcelas con manejo intensivo y, además, la broca se asoció a los parasitoides.

Un aspecto fundamental de la ecología aplicada y la conservación es la comprensión de los efectos de la intensificación agrícola en la diversidad biológica, la salud del medio ambiente y la sostenibilidad de la producción (Tilman 1999; Tilman et al. 2001). Además, el control biológico mediante la conservación tiene un potencial importante para su investigación en muchos países en vías de desarrollo (Wyckhuys et al. 2013).

En México existen casos previos de la manipulación del hábitat para promover la efectividad de las avispas parasitoides (Aluja 1999; Aluja et al. 2014), por lo que incorporar el manejo del hábitat para conservar y promover a estos insectos benéficos en los programas de manejo vigentes y futuros puede resultar en una opción viable.

## IV. Literatura Citada

Aluja M. 1999. Fruit fly (Diptera: Tephritidae) research in Latin America: myths, realities and dreams. Anais da Sociedade Entomológica do Brasil. 28(4): 565–594. doi:10.1590/s0301-80591999000400001.

Aluja M, Sivinski J, Van Driesche R, Anzures-Dadda A, Guillén L. 2014. Pest management through tropical tree conservation. Biodivers Conserv. 23(4): 831–853. doi:10.1007/s10531-014-0636-3.

Barrera JF. 2016. Café robusta, ¿héroe o villano? Ecofronteras. 20:15–17. http://revistas.ecosur.mx/Ecofronteras/Index.Php/Eco/Article/View/1661/1606.

Bosselmann AS, Dons K, Oberthur T, Olsen CS, Ræbild A, Usma H. 2009. The influence of shade trees on coffee quality in small holder coffee agroforestry systems in Southern Colombia. Agric Ecosyst Environ. 129(1–3): 253–260. doi:10.1016/j.agee.2008.09.004.

van Emden HF. 1990. Plant diversity and natural enemy effciency in agroecosystems. In: Mackauer M, Ehler LE, Roland J, editors. Critical issues in biological control. Andover, UK. p. 63—80.

Escamilla-Prado E. 2017. El banco de germoplasma de café de la UACH-CRUO en huatusco, veracruz, México. Claridades Agropecuarias.(280): 9–13.

Gómez Ruiz J, Santos Ovilla A, Valle-Mora J, Montoya Gerardo PJ. 2010. Determinación del establecimiento de parasitoides de la broca del café Hypothenemus hampei (Coleoptera: Curculionidae, Scolytinae) en cafetales del Soconusco, Chiapas, México. Entomotropica. 25(1): 25–35.

González-Moreno A, Bordera S, Leirana-Alcocer J, Delfín-González H, Ballina-Gómez HS. 2018. Explaining variations in the diversity of parasitoid assemblages in a biosphere reserve of Mexico: Evidence from vegetation, land management and seasonality. Bull Entomol Res. 108(5): 602–615. doi:10.1017/S0007485317001134.

Guharay F, Monterroso D, Staver C. 2001. El diseño y manejo de la sombra para la supresión de plagas en cafetales de América Central. Agroforestería en las Américas. 8(29): 22–29.

Infante F. 2018. Pest management strategies against the coffee berry borer (Coleoptera: Curculionidae: Scolytinae). J Agric Food Chem. 66(21): 5275–5280. doi:10.1021/acs.jafc.7b04875.

LaSalle J, Gauld ID. 1993. Hymenoptera and biodiversity. C.A.B. International (Cabi Series). https://books.google.com.mx/books?id=wKTwAAAAMAAJ.

Lomeli-Flores JR, Barrera JF, Bernal JS. 2009. Impact of natural enemies on *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) population dynamics in Chiapas, Mexico. Biol Control. 51(1): 51–60. doi:10.1016/j.biocontrol.2009.03.021. http://www.sciencedirect.com/science/article/pii/S1049964409001534.

Lomelí-Flores JR, Barrera JF, Bernal JS. 2010. Impacts of weather, shade cover and elevation on coffee leafminer *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) population dynamics and natural enemies. Crop Prot. 29(9):1039–1048. doi:10.1016/j.cropro.2010.03.007. http://dx.doi.org/10.1016/j.cropro.2010.03.007.

Mariño YA, Pérez ME, Gallardo F, Trifilio M, Cruz M, Bayman P. 2016. Sun vs. shade affects infestation, total population and sex ratio of the coffee berry borer (*Hypothenemus hampei*) in Puerto Rico. Agric Ecosyst Environ. 222: 258–266. doi:10.1016/j.agee.2015.12.031.

Mazón M. 2016. Taking shortcuts to measure species diversity: parasitoid Hymenoptera subfamilies as surrogates of species richness. Biodivers Conserv. 25(1): 67–76. doi:10.1007/s10531-015-1029-y.

Moguel P, Toledo V. 1996. El café en México, ecología, cultura indígena y sustentabilidad. Ciencias.(43): 40–51.

Monterrey J, Suárez D, González M. 2001. Comportamiento de insectos en sistemas agroforestales con café en el Pacífico Sur de Nicaragua. Agroforestería en las

Américas. 8(29): 15–21.

Pak D, Iverson AL, Ennis KK, Gonthier DJ, Vandermeer JH. 2015. Parasitoid wasps benefit from shade tree size and landscape complexity in Mexican coffee agroecosystems. Agric Ecosyst Environ. 206: 21–32. doi:10.1016/j.agee.2015.03.017.

Perfecto I, Vandermeer J, Hanson P, Carti V. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodivers Conserv. 945: 935–945. doi:10.1023/A:1018359429106.

Powell W. 1986. Enhancing parasitoid activity in crops. In: Waage J, Greathead D, editors. Insect parasitoids. 13th Symposium of the Royal Entomological Society of London, 18—19 September. London, England. p. 319—340.

Righi CA, Campoe OC, Bernardes MS, Lunz AMP, Piedade SMS, Pereira CR. 2013. Influence of rubber trees on leaf-miner damage to coffee plants in an agroforestry system. Agrofor Syst. 87(6): 1351–1362. doi:10.1007/s10457-013-9642-9.

Romero-Alvarado Y, Soto-Pinto L, García-Barrios L, Barrera-Gaytán JF. 2002. Coffee yields and soil nutrients under the shades of Inga sp. vs. multiple species in Chiapas, Mexico. Agrofor Syst. 54(3): 215–224. doi:10.1023/A:1016013730154.

Sosa-Aranda I, del-Val E, Hernández-Martínez G, Arroyo-Lambaer D, Uscanga A, Boege K. 2018. Response of lepidopteran herbivore communities to crop management in coffee plantations. Agric Ecosyst Environ. 265: 37–44. doi:10.1016/j.agee.2018.05.018.

Sperber CF, Nakayama K, Valverde MJ, De Siqueira Neves F. 2004. Tree species richness and density affect parasitoid diversity in cacao agroforestry. Basic Appl Ecol. 5(3): 241–251. doi:10.1016/j.baae.2004.04.001.

Teodoro A, Klein AM, Tscharntke T. 2008. Environmentally mediated coffee pest densities in relation to agroforestry management, using hierarchical partitioning analyses. Agric Ecosyst Environ. 125(1–4): 120–126.

doi:10.1016/j.agee.2007.12.004.

Tilman D. 1999. Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. Proc Natl Acad Sci U S A. 96(11): 5995–6000. doi:10.1073/pnas.96.11.5995.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. Science (80). 292(5515): 281–284. doi:10.1126/science.1057544.

Tooker JF, Hanks LM. 2000. Influence of Plant Community Structure on Natural Enemies of Pine Needle Scale (Homoptera: Diaspididae) in Urban Landscapes. Environ Entomol. 29(6): 1305–1311. doi:10.1603/0046-225X-29.6.1305.

Vázquez L, Matienzo Y, Veitía M, Alfonso J. 2008. Conservación y Manejo de enemigos naturales de insectos fitófagos en los sistemas agrícolas de Cuba. CIDISAV, editor. La Habana.

Wyckhuys KAG, Lu Y, Morales H, Vázquez LL, Legaspi J, Eliopoulos P, Hernandez L. 2013. Current status and potential of conservation biological control for agriculture in the developing world. Biol Control. 65: 152–167. doi:10.1016/j.biocontrol.2012.11.010.