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THE EFFECT OF AGRICULTURAL MANAGEMENT ON THE DISTRIBUTION AND ABUNDANCE OF *ARSENURA ARMIDA* (LEPIDOPTERA: SATURNIIDAE) IN CHIAPAS, MEXICO

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ABSTRACT. *Arsenura armida* plays an important ecological role in the development of woods and forests throughout Latin America. It is also consumed in several rural communities of Mexico. At present, there is no information on the host preferences of this species of moth, habitat type or the effects of human consumption on population numbers. This paper determines the effect of agricultural management on the distribution, occupation and abundance of larvae of *A. armida* in order to promote strategies for its sustainable exploitation. Six observation plots, each with an area of 4 km^2, were established in three localities of the state of Chiapas, Mexico. Three plots were subject to agricultural management (La Pimienta, La Ilusion and La Loma) and three without management (Carrizal, Huachinadero and Mirador). All host plants together with their diameter at breast height (DBH) were quantified. In order to estimate host preference, occupation, distribution and abundance, the number of larvae per tree were recorded over two consecutive years (between March and October). The occupation and abundance of *A. armida* varied among plots and the six tree species observed. Both variables presented a relationship with the mean DBH of the host species. A preference for the host species *Heliocarpus appendiculatus* and *Rollinia mucosa* was observed. The greatest abundance of larvae and host occupation was found in plots subject to agricultural management during the first year. Abundance decreased during the second year due to tree mortality. The insect presented a clustered distribution that depended on the distribution and development of host trees (highest DBH). It is suggested that host management is considered for the control of populations of *A. armida* in agricultural areas and its sustainable exploitation for human consumption.

Additional key words: Agroecosystem, edible insects, entomophagia, local adaptation

The *Arsenura* genus belongs to the Saturniidae family within the order of Lepidoptera (Peigler 1993, De Camargo et al. 2011). Their larvae attain a length of 11cm. In general, members of the Saturniidae family present a high capacity for flight, thus facilitating greater dispersal. Moth displacement generally takes place during the night to avoid water loss by evaporation and attack by predators (Palanca-Soler 1987, Amarillo 1997).

Arsenura armida (Crammer, 1779) is important for many ethnic groups in Mexico as the edible larvae are highly nutritious; they provide non-saturated fats and are an excellent source of protein (Ramos-Elorduy 1993, 2004, Ramos-Elorduy et al. 2008). They are consumed and commercialized in the Mexican states of Chiapas, Guerrero, Hidalgo, Oaxaca, Quintana Roo, Tabasco, Tlaxcala, Veracruz and Yucatan. In Chiapas, in the southeast of Mexico, this species of moth has been recorded in 31 municipalities but is only consumed in five (Morales 2010, Landero-Torres et al. 2012).

It presents a Neotropical distribution, from central and southern Mexico to southeastern Brazil and demonstrates a gregarious and aposematic behavior (Costa et al. 2004), with two generations within one year observed in some areas. The adults generally emerge between April and June and then mate immediately. One day after mating, the females oviposit between 350 and 500 eggs. The adult female lives for only six days during which it does not feed (Costa et al. 2004). Egg eclosion is associated with the start of the rainy season and maximum foliage production of the host plant with the larvae present between July and August, remaining on the same tree and feeding on its leaves during the night. The larvae can reach a length of 11 cm during the last stage when they descend to ground level to transform into a pupa (Janzen 1970).

Arsenura armida is considered as a polyphagous species (Jermy 1984, Pérez-Contreras 1999), given that they feed on at least 13 species of tree, belonging to three distinct families: *Annona montana* Macfad and *Rollinia membranacea* Triana & Planchon (Annonaceae); *Bombacopsis quinata* Jacq (Bombacaceae); *Ceiba pentandra* L. Gaertn., *Chorisia* sp., *Guazuma ulmifolia* Lam, *Guazuma tomentosa* Kunth, *Heliocarpus appendiculatus* Turcz., *Heliocarpus*

FIG. 1. Location of the study area: **A**) Carrizal; **B**) Huachinadero; **C**) Mirador; **D**) La Pimienta; **E**) La Ilusion; **F**) La Loma.

donnell-smithii Rose ex Donn., *Luehea candida* Moç & Sessé ex DC, *Theobroma cacao* L., *Pachira aquatica* Aubl and *Pseudobombax ellipticum* (Kunth) Dugand (Malvaceae) (Costa et al. 2003, Nielsen et al. 2004, Escamilla-Prado et al. 2012, Landero-Torres et al. 2012).

Most its hosts are distributed throughout the American continent and three species (*C. petandra, P. aquatica* and *T. cacao*) are also found in Europe (GBIF 2014). These species are typical of secondary semi-evergreen rain forest (Vázquez-Sánchez 1988, SEMARNAT-CONANP 2001, Orantes-García et al. 2013) and are frequently found in association with agricultural management (Escamilla-Prado et al. 2012, Landero-Torres 2012). Farmers use the host species of *A. armida* to define the border of their lands, some species are used to feed cows, as firewood and posts, even as medicinal plants. In spite of these uses, farmers do not reproduce these tree species (Escamilla-Prado et al. 2012).

The availability and nutritional quality of the hosts can affect population development, distribution and abundance of guest (Futuyma 1976, Viejo et al. 1997, Novotny et al. 2002, García-Pereira et al. 2003, Molina-Martínez & León-Cortés 2006); however, there is no data on host preference or the availability of host plant in which way has an effect on distribution and abundance of *A. armida*. In addition, the consumption of the larvae of this specie could have an impact on population development, although any potential effects are not yet known. Although highly sensitive to environmental conditions, lepidopterans can withstand changes by means of local adaptation and dispersion (García-Pereira et al. 2003, Muñoz & Amarillo-Suárez 2010, Villanueva & Saldamando 2013).

The study of the interaction between *A. armida* and its host plants is essential for the development of management strategies that promote the growth and sustainable exploitation of this lepidopteran, particularly in areas where as well as providing a source of high-protein food, it is of cultural and economic importance.

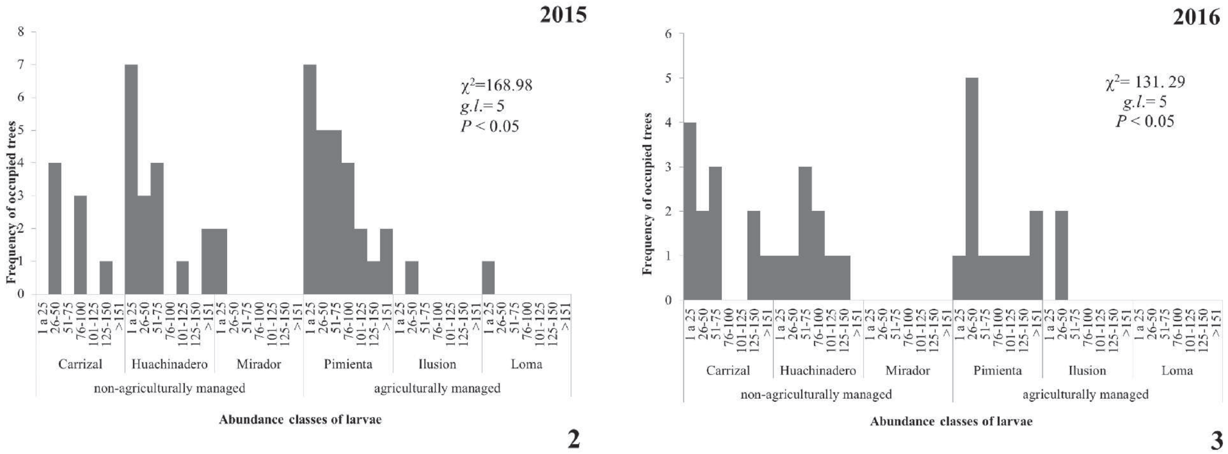
The human consumption of the larvae occurs in the months of July and August. When the larvae are not present in the field, they are stored under refrigeration for its conservation and subsequent preparation. Local and regional demand can be considered high (Escamilla-Prado et al. 2012, Landero-Torres 2012). The retail price in local markets for 2007 was $ 2.50 U.S./kg (Escamilla-Prado et al. 2012) and for 2016 it was $ 25 U.S./kg (Molina-Nery, personal observation). In some places where the insect is consumed, protocultives are carried out to achieve optimum development and commercialization (Ramos-Elorduy et al. 2008). There is evidence that *A. armida* contributes the same or more minerals than white bread, avocado, wheat germinated and menhaden fish (Ramos-Elorduy et al. 1998) and can therefore be considered as an important food source. The human consumption of larvae of *A. armida* does not cause toxicity as has been reported in birds (Janzen 1970) and what is used is the cuticle. The larvae's head and hemolymph are removed, and the body is washed and placed in boiling water for 5 to 15 minutes, thereafter they are prepared in broth or frits (Morales 2010).

In recent years, there has been a decrease in the number of hosts in plots with agricultural use, mainly due to the management of coffee plantations, maize and livestock pastures, which may affect the distribution and abundance of *A. armida*. The purpose of this research is to ascertain the influence of agricultural management on the distribution, occupation and abundance of larvae of *A. armida*, to inform local communities about the conditions that favor the emergence and proliferation of populations of this insect. This was carried out by establishing plots with and without agricultural management in areas where host plants are present. Assuming that *A. armida* tolerates high levels of perturbation (Escamilla-Prado et al. 2012, Landero-Torres et al. 2012), it is expected that this species occupies all available hosts and that abundance and distribution is homogeneous, independent of agricultural management.

MATERIALS AND METHODS

Study sites

Selected plots were either subject or not subject to agricultural management and possessed trees that are hosts for *A. armida*. A total of six sampling plots were established, located in the municipalities of Ocozocoautla de Espinosa, Huitiupan and Simojovel de Allende in Chiapas, Mexico (Fig. 1). In the first municipality, three plots were established within The Selva El Ocote Biosphere Reserve (REBISO, from Spanish name Reserva de la Biosfera Selva El Ocote). The vegetation at this site is semi-evergreen medium forest which includes several host tree species (Vázquez-Sánchez 1988, SEMARNAT-CONANP 2001, Orantes-García et al. 2013); anthropogenic disturbance is practically imperceptible, although high impact natural phenomenon, such as forest fires, can occasionally occur (Maldonado et al. 2009). The most recent forest fires were in 2003 (Table 1); however, those in 1998 resulted in significant damage to some areas of the reserve. Two of these plots are located in the periphery of the polygon of the reserve (Carrizal and Mirador) and one inside the polygon (Huachinadero), the three plots were partially affected by the fire of 1998, reason why they are formed of secondary vegetation, but none has been used for agricultural purposes. In Huitiupan and Simojovel, one and two plots were established respectively; in both municipalities host trees were present and local inhabitants were willing to conduct periodic observations in the field. The farmers harvested the trees



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FIGS. 2, 3. Frequency of occupied trees according to abundance classes (number of larvae), for *Arsenura armida*, in agriculturally managed and non-agriculturally managed plots, for each year of observation (Chiapas, Mexico): **2**, year 2015; **3**, year 2016.

TABLE 1. Geographical location, environmental characteristics and abundance of host species of *Arsenura armida* in agriculturally managed and non-agriculturally managed plots in Chiapas, Mexico. **G**, *Guazuma ulmifolia*; **HD**, *Heliocarpus donnell-smithii*; **HM**, *Heliocarpus americanus*; **HP**, *Heliocarpus appendiculatus*; **P**, *Pseudobombax ellipticum*; **R**, *Rollinia mucosa*.

Plot (municipality)	Latitude-longitude (altitude)	Abundance of hosts per plot (number of individuals)						Mean annual temperature °C^{a}	Annual precipitation mm^{a}	Natural Vegetation	Consumption of larvae	Agricultural activities
		G	**HD**	**HM**	**HP**	**P**	**R**					
Carrizal (Ocozocoautla de Espinosa)	16° 54' 37.1" 93° 38' 17.7" (824 m)	49	201		5	1	5	23.3	2145.2	High and medium semi evergreen forest	None	None. Recovering vegetation following fires of 1998
Huachinadero (Ocozocoautla de Espinosa)	16° 55' 43.4" 93° 38' 9.2" (715 m)	7	208	1	21		10	23.3	2145.2	High and medium semi evergreen forest	None	None. Recovering vegetation following fires of 1998
Mirador (Ocozocoautla de Espinosa)	16° 54' 40.1" 93° 36'47.0" (776 m)	91	10	55		23	14	23.3	2145.2	High and medium semi evergreen forest	None	None. Recovering vegetation following fires of 1998
La Pimienta (Simojovel)	17° 8' 41.1" 92° 46' 8.0" (837 m)	33	15				31	22.4	2024.3	Medium forest	High	Cattle farming, coffee groves, cornfields
La Ilusion (Simojovel)	17° 8.0' 56.1"' 92° 43"49.4" (875 m)	14	12				14	22.4	2024.3	Medium forest	High	Cattle farming, coffee groves, cornfields
La Loma (Huitupán)	17° 13' 18.4" 92° 38' 57.1" (554 m)	124	68	112				24.4	1622.1	High forest	Low	Cattle farming, coffee groves, cornfields

aSource: Servicio Meteorológico Nacional, Estaciones La Selva, Ocozocoautla de Espinosa; Simojovel y Almandro; y Huitiupán, Chiapas.

the natural forest for several years ago (at least 30), in order to have clear areas to do a variety of agricultural activities, some tree were left to delimit property boundaries. The plots with agricultural management change constantly according to the interest of the producers, just as the trees remain or are eliminated according to their usefulness in the main activity.

The three plots without agricultural management were located within the REBISO and those subject to agricultural management in the municipalities of Huitiupan and Simojovel. Each plot covered an area of 4 km^2, separated by a minimum distance of 500 m and maximum of 110 km. All the plots were visited systematically and exhaustively in order to identify the host tree species. The host species were individually georeferenced and DBH was measured during the first year of the study to estimate the development stage of each tree. Botanical samples were collected for reference and deposited in the CH Herbarium of El Colegio de la Frontera Sur (ECOSUR), San Cristobal de Las Casas, Chiapas, Mexico.

To detect the presence of larvae, each host tree was marked to conduct bimonthly observations during March-October on 2015 (year 1) and 2016 (year 2); this annual period encompasses the complete development cycle of *A. armida* (Costa et al. 2004). The location of larvae on each tree was recorded during the day, as this is when larvae are clustered together on the surface of the trunk and other woody parts of the plant. A pair of binoculars was required to record the number of larvae (tasco 8 x 30 mm-15–8x30RB, 131M/1000M) on high parts of the tree. Larvae occupation of each plot was estimated by calculating the proportion of total trees that possessed larvae during the observation period.

The consumption of larvae by inhabitants living close to the sampling plots was confirmed through direct questioning while agricultural activities within the plots were determined by observation.

Data analysis

Each annual cycle was analysed separately. Chi-squared statistical tests were performed to determine whether larvae occupation was associated with tree species and sampling plot. For this test, the presence/absence of larvae on each species of tree was considered; the test consisted of six rows (species or parcels) and two columns (presence or absence).

A Kruskal-Wallis analysis of variance (Snedecor & Cochran 1971) was performed to ascertain if abundance (number of larvae) differed significantly among plots and host species. Similarly, a χ^2 test was implemented to determine whether *A. armida* abundance per tree depended on sampling plot. Several classes of larvae abundance were established and tree frequency per class was determined.

To explore if host species development (DBH) and abundance influences the presence (occupation) and abundance of *A. armida*, a regression analysis was performed between the percentage of occupation (previously transformed by the arcsin $x^{1/2}$ function), mean DBH, and species abundance (number of trees), by plot and by species. In addition, a regression analysis of *A. armida* abundance against mean DBH and the number of trees by plot and species was carried out.

Mann-Whitney U tests were implemented to determine whether *A. armida* abundance differed between plots with and without agricultural management (comparison of two samples). All of the statistical analysis was carried out using the package IBM SPSS v. 21 (IBM Corp. 2012).

The geographical location of each tree was plotted onto a map created using the package Arc Map 10.2.1 (ESRI 2014). The data on *A. armida* occupation, collected over the whole observation period, and tree mortality, recorded during the second year, was added to the map. An analysis of the variance/mean relationship (v/m) was performed and the Morisita Index (Zarco-Espinosa et al. 2010) was obtained in order to determine the distribution of *A. armida* for each plot. The unit of observation was the abundance of larvae on the host trees in each plot. An obtained value close to 0 signified a random distribution, while a value approximate to 1 implied a uniform distribution; values above 1 indicated a clustered distribution (Badii et al. 2011, Ledo et al. 2012, De Sousa et al. 2015).

RESULTS

The host trees observed in the plots belonged to the following species: *Guazuma ulmifolia, Heliocarpus donnell-smithii, Heliocarpus americanus* L. 1753, *H. appendiculatus, Pseudobombax ellipticum* y *Rollinia mucosa* (Jacq. 1764) Baillon 1868 (Table 1). Tree abundance varied between 1 and 208 (number by plot) individuals per species/plot in the first year and between 1 and 193 in the second year. The species *G. ulmifolia* and *H. donnell-smithii* were present in all of the sampling plots, generally with a high level of abundance. The species *R. mucosa* was found in five plots but less abundant, while *H. americanus, H. appendiculatus* and *P. ellipticum* was observed in two or three plots with comparatively low abundance (Table 1). Tree mortality was observed in five plots; this was due to pests in three plots within the REBISO sample, while in the two Huitiupan and Simojovel plots, tree death was induced by local inhabitants making a cut at the base of the trunk. The dead trees in the REBISO corresponded to

TABLE 2. Diameter at breast height (DBH), tree abundance, percentage occupation and abundance of *Arsenura armida* for each year of observation (year 1 and 2), by plot type and host species, in Chiapas, Mexico.

Plot and species	Mean DBH (cm)	Abundance of trees (number of individuals)		Occupation of trees (%)		Abundance (Number of larvae)	
		Year					
		2015	**2016**	**2015**	**2016**	**2015**	**2016**
A. Mean values per plot							
Carrizal (non-agriculturally managed)	22.7	261	253	3.0	4.7	545	728
Huachinadero (non-agriculturally managed)	22.9	247	212	7.0	4.2	1151	653
Mirador (non-agriculturally managed)	11.4	193	192	1.0	0	18	0
La Pimienta (agriculturally managed)	27.8	79	74	33.0	16.2	1730	1259
La Ilusion (agriculturally managed)	24.5	40	40	3.0	5	30	88
La Loma (agriculturally managed)	8.2	304	302	0.3	0	9	0
B. Mean values per species							
Guazuma ulmifolia	13.3	318	317	3.0	0.9	554	102
Heliocarpus donnell-smithii	21.5	514	467	3.0	3.4	793	1220
Heliocarpus americanus	8.2	168	168	1.0	0	9	0
Heliocarpus appendiculatus	23.3	26	26	33.0	15.4	621	449
Pseudobombax ellipticum	8.7	24	24	0.0	0	0	0
Rollinia mucosa	26.5	74	71	28.0	16.9	1506	957

the species *H. donnell-smithii* (44) and *G. ulmifolia* (1), *H. donnell-smithii* (3) and *R. mucosa* (3) in the other plots.

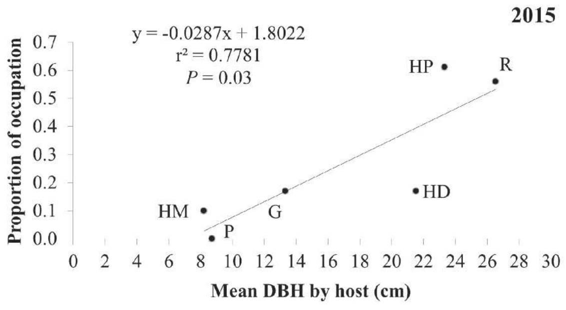
The mean diameter at breast height (DBH cm) was highest in two of the three plots with agricultural management (La Pimienta and La Ilusion) and human consumption of the larvae of *A. armida* (Table 2A). Significant differences in DBH were found between host species (Kruskall-Wallis, E= 405.78, g.l.= 4, $p<0.05$) and plots (Kruskall-Wallis, E= 568.21, g.l.= 5, $P < 0.05$). In one plot without agricultural management (El Mirador) and another with agricultural management (La Loma), mean DBH was lower, 11.4 and 8.2 cm respectively; *R. mucosa* presented a greater DBH than the other species, in particular when compared with the mean DBH of *H. americanus* and *P. ellipticum* (Table 2B).

In the first year of observations, occupation (proportion of trees observed with larvae) per plot fluctuated between 0.3 and 33% (Table 2A), while at the species level, this varied between 0 and 33% (Table 2B). Occupation by *A. armida* was significantly associated with species (year 1: χ^2= 139.42, g.l. = 5, $P < 0.0001$; year 2: χ^2= 65.87, g.l. = 5, $P < 0.0001$) and plot (year 1:χ^2= 157.51, g.l. = 5, $P < 0.0001$; year 2: χ^2= 58.80, g.l. = 5, $P < 0.0001$). In year 1, the host species with the highest level of occupation was *H. appendiculatus* followed by *R. mucosa*; in year 2, occupation was highest in *R. mucosa* followed by *H. appendiculatus* (Table 2B). The plot that presented the highest level of larval occupation, during the whole two year observation period, was La Pimienta (with agricultural management), notably higher than the other plots. A slight increase in the number of larvae was observed in two plots during the second year, one in the REBISO and the other in Simojovel; in contrast, a decrease in numbers was recorded in the remaining plots (Table 2A). *Arsenura armida* occupied three of the five available host species in the Carrizal and Huachinadero plots during year 1, one of five in El Mirador, all three species in La Pimienta and one of three in La Ilusion and La Loma. In year 2, the pattern was identical in Carrizal and Huachinadero, two out of three species were occupied in La Pimienta and La Ilusion and the insect was not present in Mirador and La Loma (Table 3).

The number of larvae varied between 9 and 1730 per plot and between 0 and 1506 per species during the first

TABLE 3. Abundance of larvae, mean larvae/tree, abundance and occupation of trees by host species of *Arsenura armida* in agriculturally managed and non-agriculturally managed plots in Chiapas, Mexico. **G**, *Guazuma ulmifolia*; **HD**, *Heliocarpus donnell-smithii*; **HM**, *Heliocarpus americanus*; **HP**, *Heliocarpus appendiculatus*; **P**, *Pseudobombax ellipticum*; **R**, *Rollinia mucosa*. **AL**, Abundance of larvae; **ML**, Mean of larvae/tree **AT**, Abundance of trees; **OT**, Occupied trees; -, host species not present.

		Year 2015						Year 2016					
		G	**HD**	**HM**	**HP**	**P**	**R**	**G**	**HD**	**HM**	**HP**	**P**	**R**
Carrizal (non-agriculturally managed)	AL	168.0	157.0	-	0	0	220.0	54.0	505.0	-	169.0	0	0
	ML	3.4	0.8	-	0	0	44.0	1.1	2.6	-	33.8	0	0
	AT	47.0	201.0	-	5.0	1.0	5.0	49.0	193.0	-	5.0	1.0	5.0
	OT	2.0	3.0	-	0	0	3.0	2.0	9.0	-	1.0	0	0
Huachinadero (non-agriculturally managed)	AL	0	235.0	0	621.0	-	295.0	0	227.0	0	280.0	-	146.0
	ML	0	1.1	0	29.6	-	29.5	0	1.3	0	13.3	-	14.6
	AT	7.0	208.0	1.0	21.0	-	10.0	7.0	173.0	1.0	21.0	-	10.0
	OT	0	7.0	0	8.0	-	2.0	0	4.0	0	3.0	-	2.0
Mirador (non-agriculturally managed)	AL	0	0	9.0	-	0	0	0	0	0	-	0	0
	ML	0	0	0.2	-	0	0.6	0	0	0	-	0	0
	AT	91.0	10.0	55.0	-	23.0	14.0	91.0	9.0	55.0	-	23.0	14.0
	OT	0	0	1.0	-	0	1.0	0	0	0	-	0	0
La Pimienta (agriculturally managed)	AL	386.0	362.0	-	-		982.0	0	448.0	-	-		811.0
	ML	11.7	24.1	-	-		31.7	0	34.5	-	-		29.0
	AT	33.0	15.0	-	-		31.0	33.0	13.0	-	-		28.0
	OT	7.0	4.0	-	-		15.0	0	2.0	-	-		10.0
La Ilusion (agriculturally managed)	AL	0	30.0	-	-		0	48.0	40.0	-	-		0
	ML	0	2.5	-	-		0	3.4	3.3	-	-		0
	AT	14.0	12.0	-	-		14.0	14.0	12.0	-	-		14.0
	OT	0	1.0	-	-		0	1.0	1.0	-	-		0
La Loma (agriculturally managed)	AL	0	9.0	0	-		-	0	0	0	-		-
	ML	0	0.1	0	-		-	0	0	0	-		-
	AT	124.0	68.0	112.0	-		-	123.0	67.0	112.0	-		-
	OT	0	1.0	0	-		-	0	0	0	-		-



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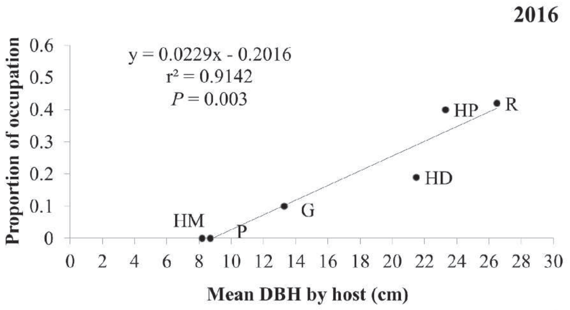

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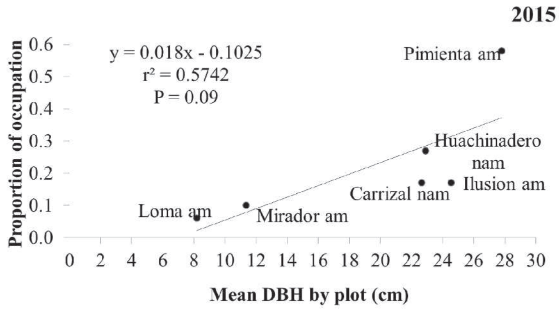

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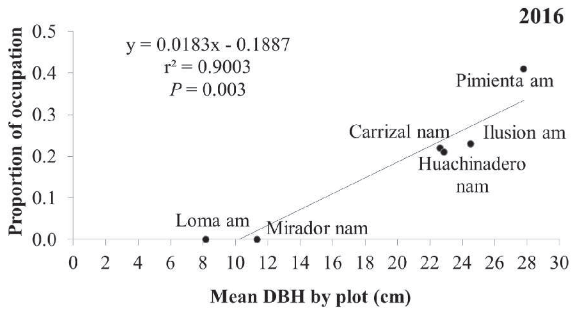

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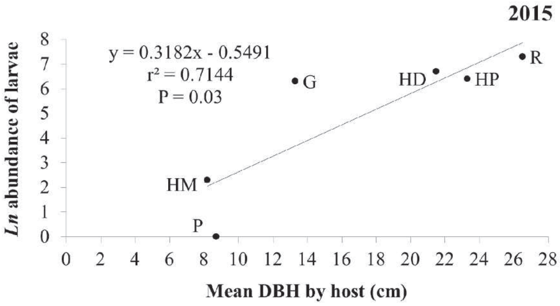

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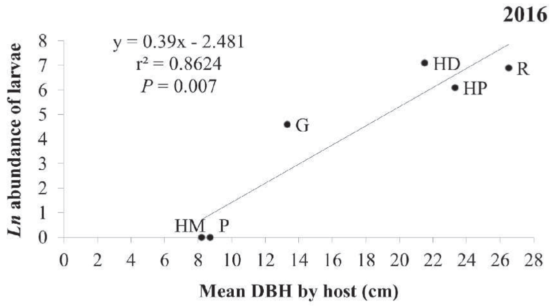

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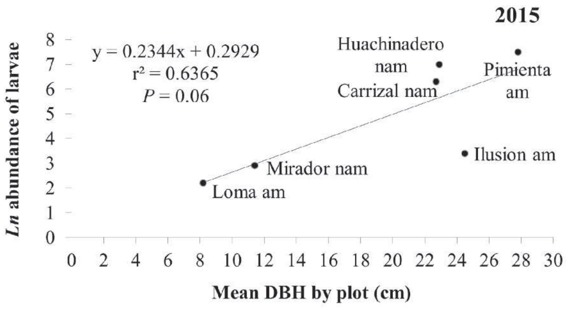

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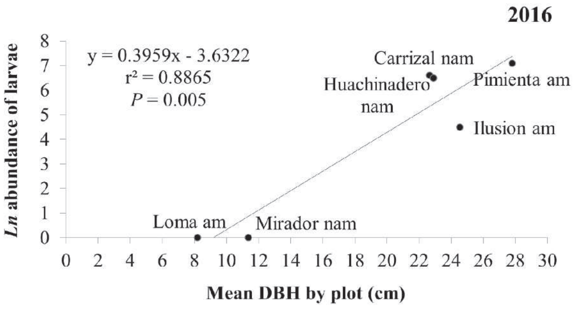

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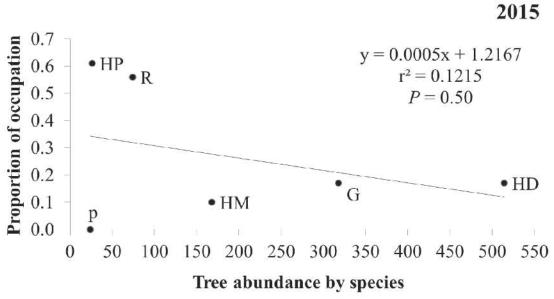
FIGS. 4–11. Lineal regression analysis of occupation (proportion of trees with larvae) and abundance of *Arsenura armida* against mean DBH by host species and plot type. **4**, Relationship between occupation of trees and mean DBH of host species in year 2015; **5**, year 2016; **6**, Occupation of trees and DBH by plot for year 2015; **7**, year 2016; **8**, Relationship between abundance and mean DBH by host species for year 2015; **9**, year 2016.; **10**, Relationship between abundance and mean DBH by plot for year 2015; **11**, year 2016 . **G**, *Guazuma ulmifolia*; **HD**, *Heliocarpus donnell-smithii*; **HM**, *Heliocarpus americanus*; **HP**, *Heliocarpus appendiculatus*; **P**, *Pseudobombax ellipticum*; **R**, *Rollinia mucosa*. **nam**, non-agriculturally managed; **am**, agriculturally managed.



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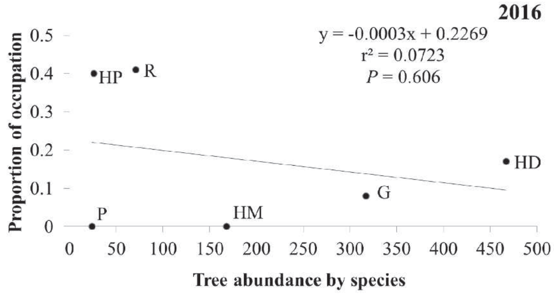

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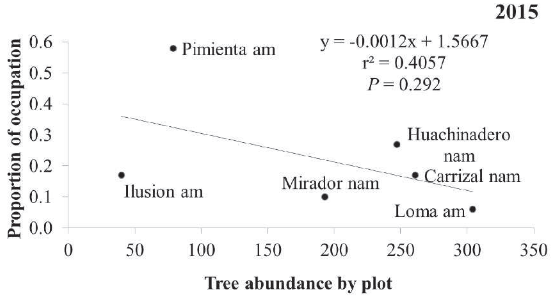

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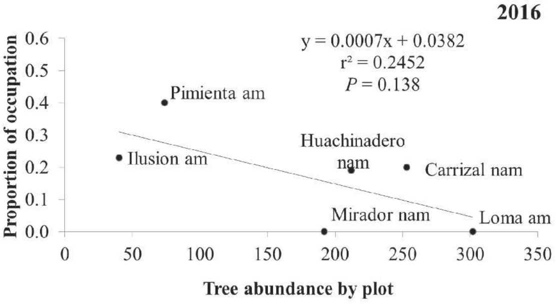

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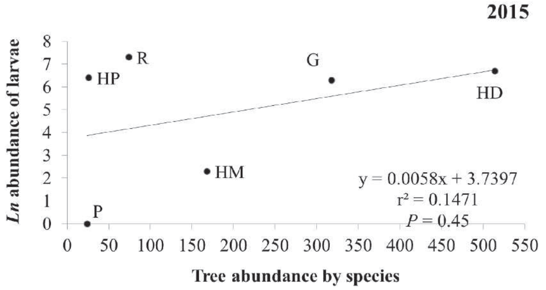

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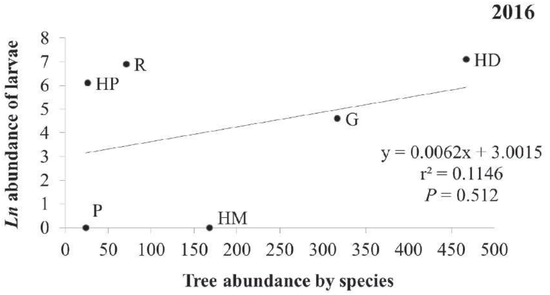

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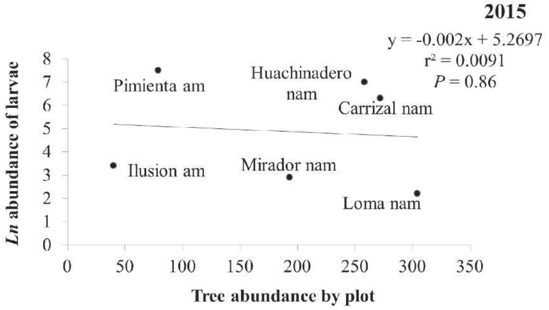

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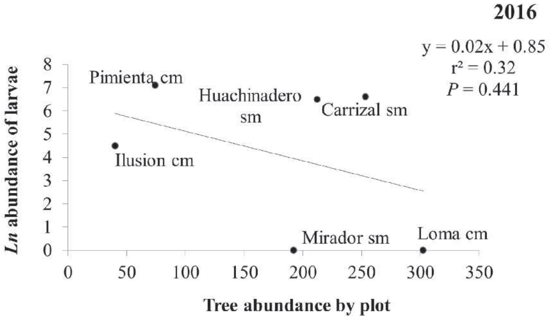

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FIGS. 12–19. Lineal regression analysis of occupation (proportion of trees with larvae) and abundance of *Arsenura armida* vs tree abundance by host species and plot: **12**, relationship between occupation of trees and tree abundance by species for year 2015; **13**, year 2016; **14**, Occupation of trees and tree abundance by plot for year 2015; **15**, year 2016;**16**, Relationship between larvae abundance and tree abundance by species for year 2015; **17**, year 2016; **18**, Relationship between larvae abundance and tree abundance by plot for year 2015; **19**, year 2016. **G**, *Guazuma ulmifolia*; **HD**, *Heliocarpus donnell-smithii*; **HM**, *Heliocarpus americanus*; **HP**, *Heliocarpus appendiculatus*; **P**, *Pseudobombax ellipticum*; **R**, *Rollinia mucosa*. The non- agriculturally managed plots are identified by "**nam**" and agriculturally managed plots by "**am**".

year of observations. In the second year, this varied between 0 and 1259 larvae per plot and 0 to 1220 per species.

Application of the Kruskall-Wallis test to the data from year one produced significant differences in abundance among plots (E = 158.454, g.l. = 5, $P < 0.05$) and host species (E = 140.116, g.l. = 5, $P < 0.05$), as did the same test with data from year 2 (plots: E = 58.973, g.l. = 5, $P < 0.05$; host species: E = 66.359, g.l. = 5, $P < 0.05$).

Throughout the two year observation period, the distribution of larvae per tree varied within and among plots (Figs. 2, 3). In year one, a few trees each with a small number of larvae were found at La Loma (Huituipan) while more trees with larvae were observed in La Pimienta (between 1 and 100 larvae per tree). No larvae were found on trees at El Mirador and La Loma during year 2. A χ^2 test detected a significant association between larvae abundance and plot for the two years' observation period (year 1: χ^2=168.98, g.l.= 30, $P < 0.001$; year 2: χ^2=131.28, g.l.= 30; $P < 0.001$).

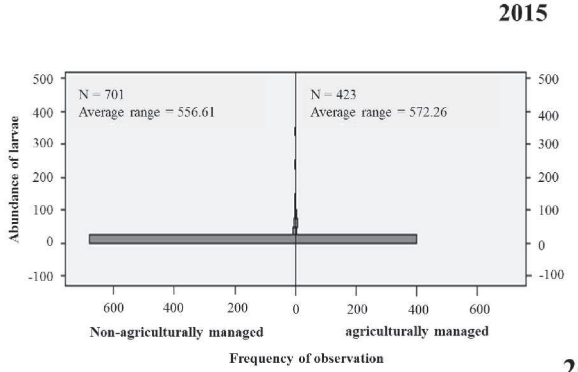
The regression analysis identified a significant relationship between occupation and mean host DBH for the two year period (Fig. 4, 5); however, there was no significant relationship between occupation and DBH per plot for year one (Fig. 6), in contrast with a significant association in year 2 (Fig. 7).

A significant relationship was found between the abundance of *A. armida* and mean DBH of host species for the two year study period (Fig. 8, 9). This relationship was marginally significant for the first year (Fig. 10) and significant for the second (Fig. 11). Occupation by *A. armida* did not demonstrate any significant relationship with tree abundance by species (number of trees) (Fig. 12, 13) or plot (Fig. 14, 15). Similarly, no significant relationship was demonstrated between the abundance of *A. armida* and tree abundance, species (Fig. 16, 17) or plot (Fig. 18, 19).

There were significant differences in larvae abundance between plots with or without agricultural management in year one (U = 153,389.5, Z= 2.094, P= 0.036; Fig. 20), but not for year two (U = 136,895.0, Z= 0.157, P= 0.875: Fig. 21). The lowest mean abundance was observed in plots without agricultural management during both years. The variance/mean relationship (v/m) and the Morisita distribution index (I_δ) was greater than one for all the plots, signifying that with respect to its host trees, *A. armida* demonstrated a clustered spatial distribution over the two year period (Figs. 22, 23, 24, 25, 26, 27).

Discussion

We are reporting by first time *H. americanus* y *Rollinia mucosa* as hosts for *A. armida*. The tree species, *Pseudobombax ellipticum* has been recognized as host (Costa et al. 2003, Nielsen et al. 2004, Escamilla-Prado et al. 2012, Landero-Torres et al. 2012), but no larvae were observed on this species. The abundance and occupation of *A. armida* varied considerably among plots, host species and number of years of observation. In the first year, plots subject to agricultural management that presented a greater mean DBH of host trees, demonstrated a higher abundance of larvae and number of occupied trees. The results suggest that agricultural management favors the occupation and abundance of *A. armida*, when the presence and growth of the host trees is not restricted. This is probably because host plants in agroecosystems



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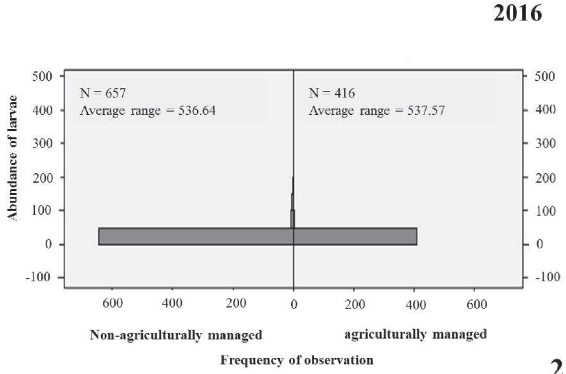

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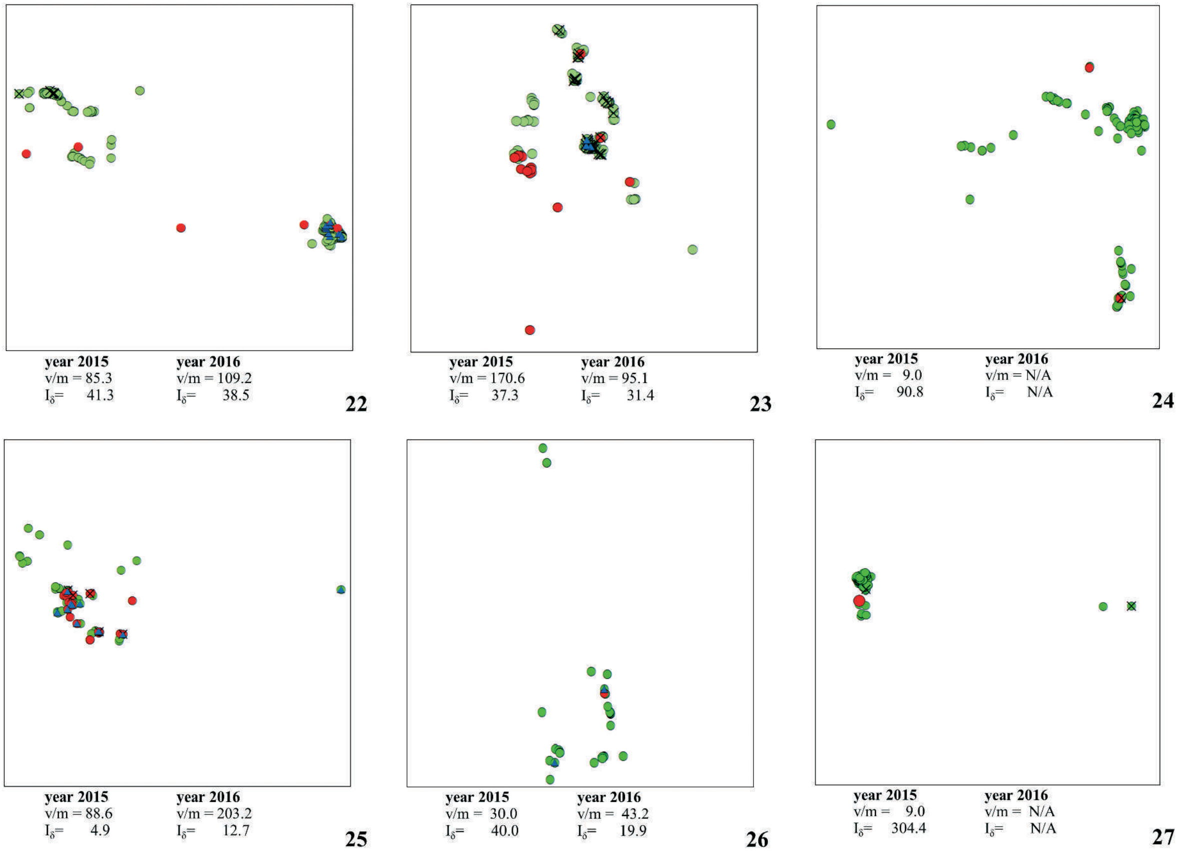
Figs. 20, 21. Results of the Mann-Whitney U test on the abundance of *A. armida* according to plot management: **20**, for year 2015; **21**, year 2016. To interpret the graph, consider that on the y axis is the range of larvae abundance assigned by the test; the x axis represents the frequency of observations of each interval. For example, for year 1, on the non-agriculturally managed for the average range 12.5, there were 682 observations and 402 with agriculturally management.



FIGS. 22–27. Distribution and occupation of host trees of *A. armida* in each plot for years' 2015 and 2016 (Chiapas, Mexico): **22**, Carrizal; **23**, Huachinadero; **24**, Mirador; **25**, La Pimienta; **26**, La Ilusion; **27**, La Loma. Host trees marked in the first year are represented by a green circle; trees occupied by larvae of A. armida in the first year (2015) are represented by a red circle; trees occupied by larvae during the second year (2016) by a blue triangle and dead trees observed in year 2016, by a "×". **22–24** represent non-agriculturally managed plots while **25–27** represent agriculturally managed plots.

are more visible and detectable by insects and can therefore be colonized more easily (Feeney 1976, Stiling 2002).

Tree mortality in plots with and without agricultural management reduced larvae abundance during the second year; this corresponded with a higher abundance of lepidopteran larvae recorded in areas with higher tree density (Vargas-Zapata et al. 2015). In our case, tree mortality not only resulted in a decrease in tree density but also represented a direct loss of *A. armida* as a local food resource. In addition, this could result in the modification of micro-environmental conditions required for larvae development (Muriel et al. 2011). This differs from other studies that have documented that although anthropogenic intervention results in a decrease in host availability, the abundance of polyphagous insects is maintained (Brown 1984, Molina-Martínez and León-Cortes 2006, Vargas & Parra 2009).

Arsenura armida larvae were more abundant on trees with a higher DBH, indicating a potential preference for mature trees probably due to their higher food availability (leaves). However, it may also be because they are more easily located by the female for oviposition or are used for mating (Pérez-Contreras, 1999). Pacheco-Flores et al. (2006) found that larvae of *Acharia extensa* (Schaus 1896) (Lepidoptera: Limacodidae) were more abundant on old trees (DAP > 88 cm), consistent with our observations on *A. armida*. There is a possibility that agricultural management allows trees to grow over a prolonged period of time. Furthermore, an absence of interspecific competition results in larger DBH than in systems subject to a lower degree of human intervention. This is evident in the relatively undisturbed forest plots of REBISO where pioneer plant species such as the host species of *A. armida*, maintain lower diameters as a consequence of the natural successional processes that take place during mature forest regeneration (Ramírez-Marcial et al. 2017).

The larvae of *A. armida* did not occupy all the trees of all the species available in the plots. The highest abundance and occupation was observed on the hosts *H. appendiculatus* and *R. mucosa*, this pattern was observed during both year l and 2. This result can be interpreted as a possible choice of the host, however data of more observation time are necessary, as well as palatability test and response to volatile compound stimuli, assuming that insect response is related to the nutrient and phytochemical content of the plants (Feeney 1976, Coley et al. 1985). Also, genetic studies are required to improve our understanding of this interaction and to discover if the plant hosts are generating a process of differentiation in populations of *A. armida*.

The distribution of trees varied according to sampling plot; highly dispersed in El Carrizal, Huachinadero and Mirador; but clustered in La Pimienta, La Ilusion and La Loma. The larvae presented a clustered, non-uniform distribution with respect to the tree hosts, that is to say the larvae were present on a few trees belonging to only several species. This could have been due to the social habits of the larvae of *A. armida*, as they remain together on the tree bark from the first to the fifth instar, forming groups of 350 to 500 individuals on only one host (Janzen 1970). However, lepidopterans with solitary habits have also displayed this distribution pattern on monoculture farms (Serra et al. 2005). In this study, between one and 329 larvae were observed on one individual tree host during year 1 and between one and 398 in year 2. The mean number of larvae per tree was higher for species *R. mucosa* (year 1: 35, year 2: 22) and *H. appendiculatus* (year 1: 30, year 2: 24).

Human consumption of *A. armida* was practiced in the communities with plots subject to agricultural management. As the majority of larvae found on the host are collected, very few individuals attain adulthood. However, the results of this research suggest that human consumption does not have a negative effect on the abundance of *A. armida*. The individuals that are undetected by collectors, predators and parasitoids are those that will maintain future generations. The surviving larvae descend from the trees, pupate in the soil and emerge the following year. In some parts of Mexico the growth of host trees in coffee plantations is allowed in order to promote the presence of *A. armida* (Landero-Torres et al. 2012) but there are no strategies for the cultivation and sustainable harvesting of *A. armida*. Our findings may eventually contribute to the development of this strategy.

In plots with agricultural management, the appearance of adult insects commenced at the start of May in while this occurred at the end of May and start of June in non-managed plots. Eclosion occurred with 15 days of difference between both types of plot. This differentiation in the biological cycle of *A. armida* could be related to environmental conditions within the plots (García-Pereira et al. 2003, Muñoz and Amarillo-Suárez 2010). In REBISO, the plots are forested and thus the environment is more humid and warmer (23 °C), while in the managed plots conditions are drier and 1°C cooler. The sustainable exploitation of *A. armida* is possible in agricultural plots, maintaining a diversity of host species that are allowed to grow to a large size (DBH approximately 20 cm).

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